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Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae)

by

(C) Felix Alexander Hermann Sperling

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Science

Department of Entomology

EDMONTON, ALBERTA
Spring 1986

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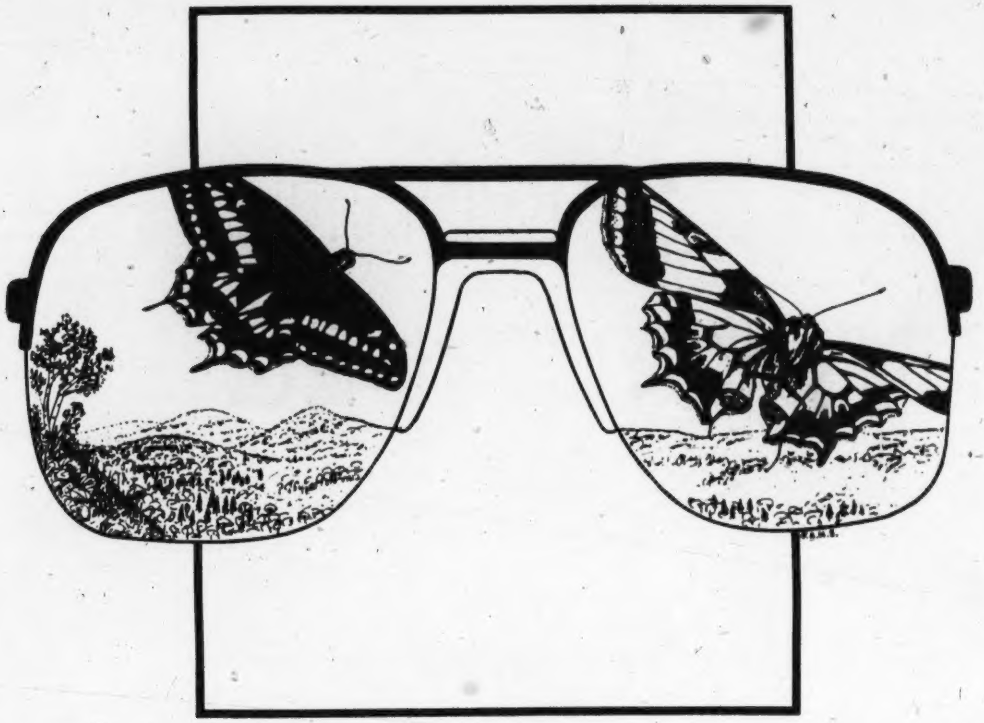

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Evolution of the *Papilio machaon* species group in western Canada (Lepidoptera: Papilionidae) submitted by Felix Alexander Hermann Sperling in partial fulfilment of the requirements for the degree of Master of Science.

Geo. E. Ball
Supervisor

John Addicott

D.A. Craig

Date...March 19, 1986....

Abstract

The *Papilio machaon* group has a broad ecological range and occurs throughout most of the Holarctic region. It contains eight species, of which the three most widely distributed live in western Canada. Most specimens of these three species (*P. machaon*, *P. zelicaon* and *P. polyxenes*) can be distinguished on the basis of morphological, electrophoretic or ecological characters. However, they hybridize frequently along zones of parapatry, as well as in restricted areas within regions of sympatry.

Taxonomic aspects of this study include the placement of all the *Artemisia dracunculus*-feeding populations of the species group as subspecies of *P. machaon*. Also *P. machaon pikei* is described as a new subspecies from the Peace River region of northern Alberta and British Columbia, with the type locality at Dunvegan. *P. m. avinoffi* and *P. kahli* are considered different expressions of hybridization between *P. machaon* and *P. polyxenes*, while *P. nitra* is treated as a genetically integrated morph within *P. zelicaon*.

Numerical analysis of characters was performed primarily with principal components analysis (PCA). Two PCAs were done separately on 10 electrophoretic loci, and 11 wing and body color characters, using the scores for the same 728 individuals. These two PCAs gave very similar relative distributions of individuals and populations, and a third PCA on the combined data set gave an enhanced separation of the major populations. Hybrid populations had intermediate

mean character values, but much broader ranges of variation than the parental species.

Other analyses corroborated this pattern. Enzyme genotypes were tested for conformance to Hardy-Weinberg proportions, and the same loci showed major interruptions in gene flow in some regions, but not in areas where hybrid swarms had formed. Discriminant function analyses on specimens collected as larvae in the wild on different foodplants support the conclusions based on PCAs and gave better species separations in some regions. Distributions of larval spot color and adult flight times suggest partial isolation between *P. machaon X zelicaon* hybrid swarms and the parental species near Calgary, Alberta. Populations of the *P. machaon* group in western Canada show a substantial degree of local adaptation to changing foodplant, climate and habitat conditions, and their interactions with these factors are described in detail in this study.

The ecological versatility and potential for rapid race formation in the *P. machaon* group can lead either to localized genetic merging or to ecological divergence and even sympatry, probably depending on the degree of ecological similarity between populations when they contact each other. Hybrid swarm formation predated habitat alteration by European settlers in central Alberta, but may have been a more recent and agriculturally related phenomenon in central Manitoba. In general, allopatric differentiation and peripheral race formation appear to account for most of the systematic structure of the *P. machaon* group. The presence of a widespread but uneven pattern of gene flow among the species of the *P. machaon* group necessitates a loose application of current species concepts, and causes considerable uncertainty in phylogenetic reconstructions.

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1. INTRODUCTION

1.1 The *Papilio machaon* Species Group

The *Papilio machaon* group is a species complex of papilionid butterflies. Adults of the group have a predominantly black and yellow coloration, and are relatively large butterflies (forewing length: 3.5 to 5.0 centimeters). The species group is generally defined by larval characters, especially a color pattern of black segmental bands and by the ability to feed on plants of the families Umbelliferae or Compositae.

The *P. machaon* group is one of 30 to 40 species groups traditionally included within the genus *Papilio*. However, recent taxonomic opinion (Hancock, 1983) has reduced the genus to just the *P. machaon* group. Since *Papilio machaon* Linneus is the type of the genus, there is little danger that the species dealt with in this thesis will ever be placed in anything other than the genus *Papilio*.

The *P. machaon* species complex has a holarctic distribution. It occurs throughout North America and in higher elevations as far south as Peru and Venezuela. It also ranges across Eurasia and is found south to South China and North Africa. The *P. machaon* group can be found in virtually any vegetation zone in this extensive region, though its habitat range is somewhat narrower in any particular area. Different ecological races have adapted to habitats as varied as arctic tundra, high altitude steppe, Saharan desert oases, temperate coastal forest, vegetable gardens and citrus orchards.

Although characterized by a great deal of ecological flexibility, the *Papilio machaon* group includes only a small number of species. Opinions about the number of species included within the group range from four (Eller, 1939) to between 10 and 20 species (numerous authors). Eight species are recognized in this study, and three of them are dealt with in detail.

There is much less difference of opinion about the limits of the group itself, with most recent authors following Monroe (1961). Most of the uncertainty about the number of species which should be recognized within the *P. machaon* group is caused by the considerable evolutionary plasticity of the group. However, differences in male genitalia, which are taxonomically valuable in many groups in the Papilionidae, are very minor in the *P. machaon* group. In North America only one species, *Papilio indra* Reakirt, can be consistently separated on this basis from the other taxa. As well, studies of populations in sympatry are uncommon, and most work has been based on samples from geographically distant localities. Comparisons among many samples often show either large phenetic or ecological differences or a confusing interplay of discordant character variation. Clearly, there is a need for intensive surveys of population variation in regions of sympatry or parapatry between major species of the *Papilio machaon* group.

The primary objective of the present study is to survey the *P. machaon* group in western Canada, and to understand its evolution. I have concentrated on determining how many species and subspecies occur in western Canada, and describing the morphological, genetical and ecological distinctions among them.

1.2 Historical Perspective

Scientific work on the *P. machaon* group presents a surprizingly representative series of examples of important stages in the development of systematics as a separate discipline. The recognized starting point for modern taxonomy, Linneaus' *Systema Naturae*, Tenth Edition, (1758), contained the description of *P. machaon* itself. New names such as *P. polyxenes* (Fabricius, 1775) and *asterius* (Stoll, 1782) were also published in that early period of endeavor to provide a full description of nature and what was perceived as God's works.

As western societies proceeded in their economic conquest and biological exploration of the remaining parts of North America and Eurasia, there followed a steady stream of taxonomic descriptions. These provided a sense of the primacy of order, and the security and power of knowledge, for the people who received the spoils. In addition, the practice of figuring the name of the author prominently behind the name of a taxon ensured that considerable effort and money was expended in the race to acquire this form of immortality. *Papilio zelicaon* was described by Lucas in 1852 under such circumstances, edging out Boisduval's *P. zolicaon* by a matter of a few months (Dos Passos, 1962). Obviously new species were exhausted relatively quickly, while the plethora of geographic races in the species of the *P. machaon* group provided an excuse for new names that has not been exhausted to this day. Subspecies names became fashionable around the turn of the last century and many of the older names were subsumed under the very oldest ones. The most recent treatment of *Papilio machaon* throughout Eurasia (Seyer; 1974,1976a,1976b,1977) recognizes 36 subspecies in that region alone and synonomizes many more names.

The opening up of western North America in the latter part of the 1800's was integrally associated with many new names. *P. machaon aliaska* was contributed by Scudder in 1869, based on material collected by an American lieutenant in a "Russo-American Telegraph Expedition" to Alaska. W.H. Edwards added a number of other names in the same sort of environment. He became wealthy through investments in the expanding railway industry of this period, and his financial security allowed him to play an important role in North American butterfly taxonomy. To the *Papilio machaon* group he contributed the names *P. bairdii* (1866), *P. oregonius* (1876) and *P. nitra* (1884), among others. The precise placement of many of these taxa remains uncertain to this day, and some of them will be dealt with in this study.

The discovery and classification of new taxa saw a climax of sorts in the Victorian era. The plethora of specimens led to a new understanding of the basis for their inexhaustible variation and yet also to a philosopical rift among taxonomists. Darwin's publication of **The Origin of Species** (1859) provided a starting point for this process. By 1883 W.H. Edwards was arguing that criticism of his species designations in the *P. machaon* group was tantamount to a refusal of the teachings of Darwin, which was in turn equivalent to failing to admit the truths of Copernicus. Yet in his zeal to defend his taxonomy, he failed to see the importance of the forms intermediate between *P. oregonius* and *P. zelicaon* which Hagen (1882) found in the Pacific Northwest. Instead he chose to concentrate on the regions he was familiar with, where *Papilio zelicaon* did not appear to hybridize with any other populations.

Edwards' case for specific distinction between these taxa was greatly strengthened when Davis Bruce found that larvae of *P. bairdii* fed on *Artemisia dracunculus* Linneaus in the larval stage (Edwards 1893 and 1895). This foodplant is a member of the Compositae, rather than the Umbelliferae or Rutaceae which larvae of *P. zelicaon* feed on. Also Bruce found that, in Colorado, *P. bairdii* adults were polymorphic for a yellow wing form which was much more like that of *P. oregonius* and *P. zelicaon* than the mostly black form it had previously been known for. However, Edwards' (1895) taxonomic response was to describe the yellow form from

Colorado as yet another new species, *Papilio brucei*. This conflict between an increasing understanding of evolutionary phenomena such as polymorphism and the need for comprehensible, consistent classifications has continued to provide friction a century later.

One of the men who was in many ways the epitome of acquisitiveness in the dying days of Victorian thought, Lord Walter Rothschild, also played a role in the systematics of the *P. machaon* group. His curator, Karl Jordan, contributed substantially to putting taxonomic practice in better accordance with evolutionary principles such as geographic differentiation (Mayr, 1955). They worked together on the Papilionidae, where they consistently and accurately applied the concept of geographic races to their formal recognition of subspecies. Interestingly enough, they saw some specimens from west of Calgary from the same *P. machaon X zelicaon* hybrid populations which piqued my own interest in the group. They continued to use relatively traditional assignments, but remarked on the close resemblance of the black individuals from this area to the black forms of *P. bairdii* (Rothschild and Jordan, 1906).

The 1930's saw a fresh burst of new names proposed for taxa within the *P. machaon* group. Several of these were described from western Canada and Alaska. A.H. Clark (1932) contributed *P. machaon hudsonianus* from the boreal zone of northern Manitoba and Ontario, and *P. machaon petersi* from Alaska. Chermock and Chermock (1937) described *P. machaon* race *avinoffi* and *P. nitra* form *kahli*, both from the Riding Mountains of central Manitoba. McDunnough (1939a) described *Papilio machaon dodi* from the prairies of southern Alberta and Saskatchewan. A number of new taxa were also described for the rest of North America during this period, while Eller (1936) produced a major monograph on the races of *Papilio machaon* in Eurasia. Eller (1939) followed this with a shorter treatment of the *P. machaon* group worldwide, in which he proposed classifying all North American taxa except *P. indra* as subspecies of *Papilio machaon*.

The names *P. machaon avinoffi* and *P. m. petersi* are now generally accepted as synonyms of *P. m. hudsonianus* and *P. m. aliaska*, respectively. *P. m. dodi* is accepted as a valid taxon, but is variously placed as a subspecies of *P. machaon*, *P. bairdii*, or *P. oregonius*. *P. nitra* form *kahli* was elevated without explanation to species status by Wilson (1961) and has generally continued to be used in that manner. Eller's work found no acceptance in North America, and instead was cited as an example of poorly informed taxonomy (Remington, 1968a). In general the work of the 1930's served as an extension of the exploratory trend of earlier periods.

During the late 1950's, an understanding of the *Papilio machaon* group was placed on a rather different footing. The technique of mating *Papilio* by hand was described in detail by Clarke (1952), and Clarke collaborated in obtaining numerous hybrids in the following years, many of them within the *P. machaon* group (Clarke and Knudsen, 1953; Clarke and Sheppard, 1953, 1955a, 1955b, 1956a; Clarke *et al*, 1977). Hand pairing became a commonly used technique in hybridizing even distantly related species within the genus *Papilio*. The papers which Clarke co-authored with Sheppard have been the best studies to date on the genetics of the adult and larval color patterns of various taxa within the species group. They extended their hybridizing experiments to other species of *Papilio* and produced a number of classic works, including studies on the African mimetic complex of *Papilio dardanus*. (The understanding of the interactions of genes which was gained from these hybridizing experiments was applied to the prevention of rhesus haemolytic disease in newborn humans, and Clarke was eventually knighted for his work.)

In the United States, Remington also conducted numerous hybridization and rearing experiments on the *Papilio machaon* group. His first report (1956) on this work was concerned with a collecting trip made to the Riding Mountains to obtain *P. kahli*, but he did not fully publish any of this research. His last report (1968) included a description of a new species closely allied to *P. zelicaon*. The separation of Remington's *P. gothica* (1968) was based on the hybrids it produced, as well as slight color pattern and ecological differences from *P. zelicaon*. Sibling species were in fashion in the evolutionary biology and systematics of the time, since they provided a kind of confirmation of the primacy of genetic considerations in species definitions.

However, Remington's *P. gothica* was soon criticized for a variety of reasons (Clarke and Sheppard, 1970; Shapiro, 1975; Emmel and Shields, 1980) and the only remnant of his concept survived in the form of a subspecific division of *Papilio zelicaon*. The name of that division was later changed to *P. zelicaon nitra*, on the basis of rearing studies by Fisher (1977) which showed that the taxon described by Edwards was just a dark form of *P. zelicaon*. Fisher theorized that the black form had arisen through the introgression of genes from *P. polyxenes*, a suggestion in correspendence with Remington's (1956, 1958) earlier thoughts on the origin of *P. nitra* form *kahli* through hybridization between *P. machaon* and *P. polyxenes*.

One of Remington's students, S. Ae, carried out numerous hybridizations of *Papilio* species, using the hand pairing technique of Clarke (1952). He continued this work for more than two decades in Japan, publishing numerous progress reports and culminating in a major paper on *Papilio* phylogeny (Ae, 1979). He showed that even relatively distant interspecific crosses could produce adults, and many crosses between species within the *Papilio machaon* group had a reasonable degree of F1 viability. Ae's work is the tip of a veritable iceberg of *Papilio* hybridization studies, carried on by numerous enthusiasts, usually amateur, who rarely if ever publish. Similar situations can be found in saturniid and killifish circles, where the considerable effort to do such work seems to be maintained by a joy derived from the creation of new kinds.

During the last 15 years a substantial number of publications have appeared on the ecology of various members of the *Papilio machaon* group. These include studies on oviposition behavior (eg. Wiklund, 1981), larval growth (eg. Scriber and Feeny, 1979) and diapause dynamics (eg. Sims, 1980), among others. Although addressed primarily to a mainstream ecological audience, they demonstrate a diversity of mechanisms allowing different populations within species of the *P. machaon* group to adapt to local ecological selection regimes. A consequence of these studies to those that are more systematically oriented is that they show how numerous ecological races could have arisen, some within the last century (Shapiro and Masuda, 1980), and yet may still be little more than variations derived from a single basic gene pool.

Considering the ecological and genetic complexity of the *Papilio machaon* group, it may well be futile to expect sytematic research on it to have simple taxonomic consequences. As well, the history of human research on the group can bias a clear understanding of its systematic structure. In this study, my primary focus will be on describing and explaining the pattern of phenetic variation within and between populations of the *P. machaon* group. My assignment of names to parts of this genetic system is guided mainly by how much those names enhance our ability to efficiently communicate information about it.

2. MATERIALS AND METHODS

2.1 Acquisition of Specimens

2.1.1 Collections examined

I borrowed specimens from and examined the collections of several individuals and institutions. These are listed in Table 1, below. The curators of institutional collections are listed at the ends of entries. I examined about 2000 specimens from collections other than my own, and 1200 from my own.

The majority of the material collected by myself during this study, including the holotype and a series of paratypes of *P. machaon pikei*, will be deposited at the Canadian National Collection, Ottawa. Voucher specimens have been deposited at the University of Alberta Strickland Museum, as well as locality listings for all specimens examined in the course of this study.

Table 1. Collections examined.

AME	Allyn Museum of Entomology, Sarasota, Florida, 326111 U.S.A. (L.D. Miller)
APME	Alberta Provincial Museum, Natural History Dept., 12845-102 Ave., Edmonton, Alberta, T5N OM6 Canada (A.T. Finnemore)
ACORN	J.H. Acorn, Dept. of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada
BIRD	C.D. Bird, Box 165, Mirror, Alberta TOB 3C0 Canada
BCPM	British Columbia Provincial Museum, Parliament Building., Victoria, British Columbia, V8V 1X4 Canada (R.A. Cannings)
BMNH	British Museum (Natural History), Cromwell Road, London, SW7 5BD, England (R.I. Vane-Wright)

CIBAROWS	J.H. Cibarowski, Department of Biology, University of Windsor, Windsor, Ontario, N9B 3P4 Canada
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Research Branch, Ottawa, Ontario, K1A 0C6 Canada (J.D. Lafontaine)
FAHS	F.A.H. Sperling, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada
GIBBON	Department of Entomology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2 Canada (R.E. Roughley)
GUPPY	C.S. Guppy, 4120 St. Georges Ave., North Vancouver, British Columbia, V7N 1W8 Canada
HILCHIE	G.J. Hilchie, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada
HOOPER.D	D.F. Hooper, Somme, Saskatchewan, S0E 1N0 Canada
HOOPER.R	R.R. Hooper, Box 205, Fort Qu'Appelle, Saskatchewan, S0G 1S0 Canada
KIMMICH	H.P. Kimmich, 3372 Mahon Av., North Vancouver, British Columbia, V7N 3T6 Canada
KLASSEN	P. Klassen, Box 212, Elm Creek, Manitoba, R0G 0N0 Canada
KOHLER	S.J. Kohler, Forest Insect and Disease Section, Montana Department of Natural Resources and Conservation, 2275 Spurgin Road, Missoula, Montana, 59809 U.S.A.
KONDLA	N.G. Kondla, 22 Brock Place, Lethbridge, Alberta, T1K 4C7 Canada
KRIVDA	W. Krivda, 319 Crossley Ave., The Pas, Manitoba R9A 1B7 Canada
LIPPESCH	Lippesches Landesmuseum, Ameide 4, D-4930 Detmold 1, Federal Republic of Germany, (R. Springhorn)
PIKE	E.M. Pike, Box 1231, Fairview, Alberta, T0H 1L0 Canada
REIST	J.D. Reist, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, R3T 2N6 Canada
ROM	Department of Entomology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario, M5S 2C6 Canada (R. Jaagumagi)
SHAW	K.A. Shaw, 7816 148 St., Edmonton, Alberta, T5R 0Z2 Canada
SHEPARD	J.H. Sheppard, Sproule Creek Road, RR#2, Nelson, British Columbia, V1L 5P5 Canada
SHIGEMAT	S. Shigematsu, 2314-22nd St. S., Lethbridge, Alberta, T1K 2K2 Canada
SPMR	Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan, S4P 3V7 Canada (R.R. Hooper)
THORMIN	T.W. Thormin, Alberta Provincial Museum, Natural History Department, 12845-102 Ave., Edmonton, T5N 0M6 Canada
TROUBR.	J. Troubridge, RR#1 Cayuga, Ontario, N0A 1E0 Canada
UASM	Department of Entomology, University of Alberta,

	Edmontom, Alberta, T6G 2E3 Canada (G.E. Ball & D. Shpeley)
UBC	Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver British Columbia, V6T 2A9 Canada (S. Cannings)
UCalgary	Biology Department, University of Calgary, Calgary, T2N 1N4 Canada (G. Pritchard)
UMan	Department of Entomology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2 Canada (R.E. Roughley)
Wat.NP	Waterton National Park, Interpretation Administration, Waterton, Alberta, T0K 2M0 Canada

2.1.2 Collecting adults

During the summers of 1980 through 1984 I collected about 650 adults of the *Papilio machaon* group, mostly in Alberta and northern British Columbia. These were caught with a net with a 35 cm hoop diameter and placed into glacine envelopes. A few were killed immediately, by pinching their thorax. Most were kept alive on ice for transport back to Edmonton, where they were frozen at -20 C and eventually used for electrophoresis. Adult specimens lived for 7-10 days on ice, and so there was little difficulty in bringing back material from collecting trips of a few thousand kilometers. Eventually all specimens were pinned and dried with their wings spread in the manner standard for Lepidoptera curation.

Species of the *Papilio machaon* group were relatively uncommon in western Canada, and most specimens collected in the wild were males taken on hilltops and prominent river bank edges. Few females were taken on hilltops, and most were in copula or being pursued by males when they were found there. They formed a much higher proportion of the total catch in valley bottoms and along roadsides, where the larval foodplants usually occurred, but still remained very hard to find.

The best collecting on hilltops occurred at 12:00 to 17:00 hours, though I occasionally took individuals perching or basking after 19:00 hours in northern Alberta. Usually between one and five *P. machaon* butterflies were at any one particular hilltop, and these could be collected in less than an hour. Many individuals that had been scared off returned within a half hour, and a number of butterflies could be collected again on the hilltop even if no individuals had been seen to escape. For this reason it was found to be most efficient to visit several hilltops in an area in succession, and to return once or twice to each. The best hilltops were prominences which could be sighted from a distance of 10-20 km and had bare patches and nectaring sources on top. I found forestry lookouts and radio tower hills to be especially easy to collect on, since most were accessible by vehicle.

For my study, I tried to obtain as many specimens as possible from each of a number of localities located in a rough grid pattern with intervals of 150-200 km across Alberta and northern British Columbia. I was able to collect 20 or more adults from most of these localities, though I had to return to several of them a number of times in different years to do so. These localities comprise much of the geographic survey portion of my study, and are compared to more widely spaced localities in the remainder of western Canada and adjacent United States. I was able to sample most of the Alberta and northern British Columbia localities several times throughout the summer, and made a point of collecting larvae below the hilltops where adults had been taken earlier in the summer. Some population samples include adults obtained from larvae collected within about five km of a hilltop locality, as well as specimens from the hilltop itself. They have been distinguished from the wild-collected adults in the sections dealing with foodplant associations. Where ever possible, material taken by other collectors at or near a major locality was included in the morphometric portion of my study.

In total I drove more than 120,000 km to collect adults and larvae for this study, and about half of this distance was travelled in Alberta.

2.1.3 Larvae

I collected about 1800 larvae during 1980-1984, and attempted to rear most of these to the adult stage. All of these larval records are listed in Table 20. About 450 reared adults were obtained. These allowed me to relate adult structural and electrophoretic characters to larval foodplant and habitat. Most of the females I collected were obtained by rearing wild-collected larvae, which generally gave close to an even ratio of males and females.

For some samples, I obtained pupae through the mail from other collectors (also listed in Table 20). These included all the samples used in electrophoretic analysis for *P. polyxenes*, as well as most of the *P. polyxenes X machaon* hybrid zone material and all the *P. zelicaon* specimens from Abbottsford, British Columbia.

During the study period, I made an effort to regularly check potential host plants for larvae, both during trips made to collect adults as well as trips made solely for collecting larvae. I tried to check as wide a variety of umbellifers and *Artemisia* species as possible, and found that most larvae were on isolated plants at the edge, rather than the middle, of large foodplant patches. Most of the potential foodplants are colonizers that grow well in disturbed habitats, and so roadside ditches and old fields were the best sites for collecting larvae. Larvae were usually found by scanning foodplants for feeding damage to the leaves, though on *Zizia* plants it was necessary to inspect the underside of each umbel.

Suggestions of other field collectors were followed in seeking out localities which were a reliable source of larvae. Also, published records for other regions and my increasing awareness of the pattern of variation in local foodplant use were of help in finding larvae. However, such matters also influence which foodplants are checked most frequently, and so in my interpretations I have concentrated on those patterns that are well supported by a number of separate observations.

Identification of instars was based generally on the presence of spines, the presence of mature banding pattern and relative head capsule size. The criteria of Perkins *et al* (1968) were generally employed, but were only partially reliable, especially for distinguishing first and second instars. Color pattern and spine length of fourth instar larvae was particularly variable, even in local populations.

Samples of all new foodplant records were pressed and submitted for identification by Dr. G.J. Packer, Department of Botany, Unversity of Alberta. Voucher specimens were not kept for most of my own records, since the plant species involved were close to unmistakable after an initial familiarity had been gained. Records attributed to people other than myself were identified by those people. I have included them in Table 19 because they had been published and required discussion, or because they seemed reasonable, based on my own experience.

Many larvae were reared on the foodplant they were found on. Batches of larvae from different localities were kept separately in Frig-O-Seal® plastic containers and fresh foodplant clippings were added about every two days, or more often if stale. Refrigerated foodplants served for about two weeks before larval mortality started to increase noticeably. Larval mortality due to disease was sometimes high, especially when the foodplant was replaced by another species or even taken from another locality. Also jostling and temperature changes during trips on back roads, as well as stale foodplant, contributed to mortality during collecting trips. For these reasons the number of adults obtained from different batches of larvae (Table 20) is not a reliable indicator of relative suitability of foodplants.

After collection, most larvae were reared ~~at~~ room temperatures of 20-25 C with only minor fluctuations in daily cycles. Light periods were usually about 17 hours. Fresh pupae were left under these conditions for 2 to 4 weeks before being placed in a dark refrigerator at 0-4 C. Pupae under refrigeration were misted with water every few weeks and removed in 2-4 months for emergence. Pupae were then placed in glass jars, misted every 2-3 days and kept at 20-25 C with light periods of 14.5-20 hours. Pupae which did not emerge under these conditions after about 3 months, and which were not obviously dead, were put through another cool cycle of 4-6 months duration. Most of these emerged during the next emergence period, though a few went through 3 cool cycles before emerging. I assumed that pupae reared by other people had been through a cool period already. These were allowed to emerge immediately upon receipt through the mail.

2.2 Characters examined

2.2.1 Morphometric characters

Eleven morphometric characters were used in this study. These are defined in Table 2, and illustrated in Figures 1 to 6. Only specimens for which each of these characters could be scored were used in the multivariate analyses. Wherever possible, the right side of the specimen was used.

The choice of characters for analysis was made for a number of reasons, of which the following were the most important:

1. The characters had been used previously by other workers for distinguishing between species. Those listed by Remington (1968a), were especially useful in this regard, because of the clear manner in which they were defined. This allowed me to relate populations in western Canada to particular species concepts developed elsewhere in North America, and also to test diagnostic characters against variation in electrophoretic characters.

2. The characters had to be fast and easy to score by eye, and hence allow accurate processing of numbers of specimens in a relatively short time.

3. There had to be a large amount of variation in character states expressed in the major study area, western Canada. The purpose of this criterion was to maximize the likelihood that useful information would be recorded when a character was scored.

4. Characters were chosen which appeared to vary fairly independently of each other within populations, to maximize the likelihood of sampling the effects of several different genes, and hence of obtaining information of significance to gene flow between populations. I tried to minimize the

Table 2. Descriptions of morphometric characters.

Numbering of character states is the same as that used in multivariate analyses.

A. Extent of yellow scaling in cell Cu2, in anal margin of dorsal hindwing (Fig. 2)
  1. All except a few yellow scales are restricted to area from inner margin of median dark band to less than halfway to divergence of veins Cu2 and Cu1. (eg. Fig. 3)
  2. Virtually all yellow scales restricted to area between median band and divergence of Cu1 and Cu2.
  3. Yellow scales extend past junction of Cu1 and Cu2, but less than halfway between Cu1-Cu2 junction and wing base.
  4. Yellow scales extend from median band to more than 3/4 of way to wing base. (eg. Fig. 2)

B. Shape of pupil in anal eyespot of dorsal hindwing. (Fig. 1)
  1. Thin line at lower edge of blue region, connected to wing margin. (eg. Fig. 1a)
  2. Club shaped, in that thinnest portion near margin is less than half the width of thickest portion closer to center of eyespot. (eg. Fig. 1b, 2, 3)
  3. Oblong spot at lower edge of red area, not connected to margin. (eg. Fig. 1c)
  4. Round spot centred in red area, generally with less than two times as much red above pupil as below it. (Fig. 1d)

C. Extent of black scales between blue and red portions of anal eyespot of dorsal forewing. (Fig. 1-3)
  1. Black line extending along less than 1/4 of blue-red boundary. (eg. Fig. 1a)
  2. Black line separating blue from red along between 1/4 and 3/4 of the width of anal eye. (eg. Fig. 1c)
  3. Black line separating more than 3/4 of blue from red (boundary line may be wide or narrow).(eg. Fig. 1b,1d,2,3)

D. Color of hairs on tegula. (Fig. 4 and 6)
  1. Virtually all hairs on tegula yellow. (eg. Fig. 4a-b and 6a-e)
  2. Less than half as much yellow on tegula as in typical yellow morph adults but more than about 15%. (eg. Fig. 4c)
  3. Virtually all tegula hairs black. (eg. Fig. 4d)

E. Extent of yellow scales in basal half of disc of central forewing. (Fig. 5)
  1. Yellow scales in more than 50% of area. (eg. Fig. 5a)
  2. Thick streaks or a more general flush to less than 50% of total area. (eg. Fig. 5b)
  3. Few thin streaks or a light sprinkling of yellow scales. (eg. Fig. 5c)
  4. Virtually no yellow scales in basal half of disc of ventral forewing. (eg. Fig. 5d-e)

F. Extent of yellow scales of postmedian yellow band in apical cell of ventral forewing. (Fig. 5)
  1. Postmedian spot large, occupying more area than bordering black scales. (eg. Fig. 5a-c)
  2. Definite patch of diffuse yellow, but occupying less area than black black scales. (eg. Fig. 5d)
  3. Virtually no postmedian yellow scales in cell. (eg. Fig. 5e)

Table 2. continued.

G. Number of cells with orange patch in postmedian area of ventral hind wing. (Fig. 3)
1. No cells with a distinct patch of orange cells on distal side of postmedian yellow area.
2-8. The total number of cells, plus one, which have a distinct patch of orange, up to a total of 7 cells. Postmedian wing cells which are covered in only black scales are assumed to have an orange patch, as in some female *P. polyxenes*.

H. Amount of yellow hair on metathorax below base of hindwings. (Fig. 6)
1. Yellow hairs extend around the ventral part of metathorax. (eg. Fig. 6a)
2. Substantial patches of yellow hairs on each side of metathorax which do not meet ventrally. (eg. Fig. 6b-d)
3. All metathoracic hairs black, or at most a very few short yellow hairs restricted to immediate base of wing. (eg. Fig. 6e-f)

I. Ventral abdominal line. (Fig. 6)
1. All abdominal segments with distinct ventral line of yellow hairs along saggital plane. (eg. Fig. 6a)
2-9. The total number of segments, plus one, which do not have a distinct patch of yellow scales or hairs along saggital line. Start counting from first abdominal segment after thorax, to a maximum of 8.

J. Lateral abdominal yellow. (Fig. 6)
1. Broad band of yellow on each side, extending along length of abdomen (male claspers excluded). (eg. Fig. 6a-d)
2. Large square lateral spots on some or all abdominal segments, with narrow divisions between spots. (eg. Fig. 6e)
3. Small round lateral yellow spots on all or most segments, distance separating spots generally greater than width of spots. (eg. Fig. 6f)

K. Upper abdominal spots. (Fig. 6)
1. All abdominal segments with a distinct pair of subdorsal yellow spots, separated from lateral abdominal band or line of spots (character J., above). (eg. Fig. 6e-f)
2-9. The total number of segments, plus one, which do not have at least one yellow spot distinct from yellow line.

Figures 1 to 4.

Figure 1. Anal eyespot of dorsal hind wing.

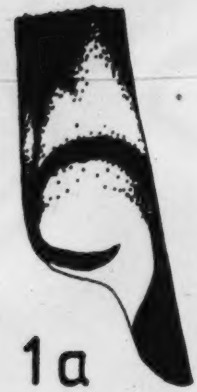
- a. *P. m. aliaska*. Mi. 391, Alcan Hwy., British Columbia.
- b. *P. m. dodi*. Nacmine, Alberta.
- c. *P. zelicaon X machaon*. Nacmine, Alberta.
- d. *P. zelicaon*. Wintering Hills, Alberta.

Figure 2. Yellow scaling of dorsal hindwing anal margin. *P. m. oregonius*, Brewster, WA. Character states for yellow anal scales are numbered beside figure.

Figure 3. Ventral hindwing, with location of orange scales. *P. p. asterius*, Karlsruhe, North Dakota. Arrow shows postmedian band, which contains orange scales.

Figure 4. Dorsal view of thorax, showing tegula.

- a. *P. zelicaon* yellow morph. Wintering Hills, Alberta.
- b. *P. zelicaon X machaon* black morph. Bragg Creek, Alberta.
- c. *P. p. asterius*. Karlsruhe, North Dakota.
- d. *P. p. asterius*. Karlsruhe, North Dakota.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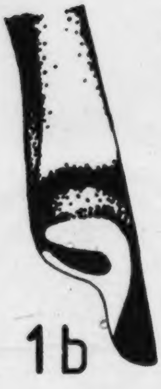
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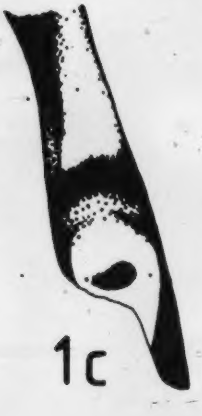
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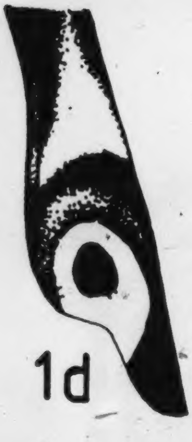
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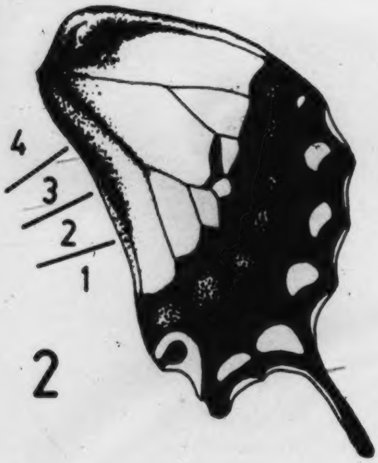

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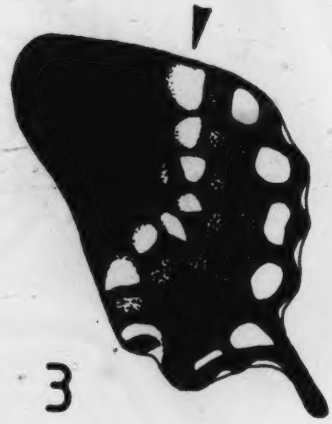
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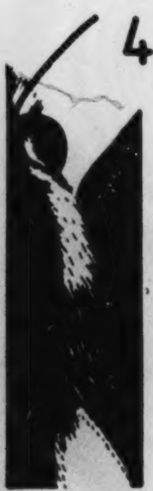
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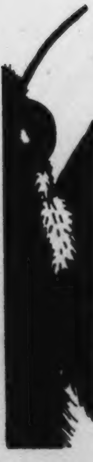
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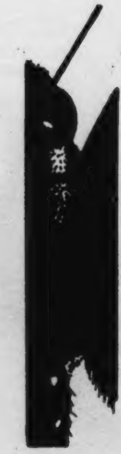
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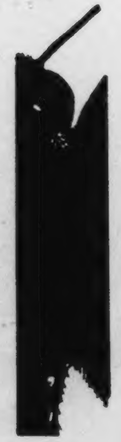

4d

Figure 5. Yellow scales on disc and apex of ventral forewing. Arrows on Figure 5b show location of disc and apical cell.

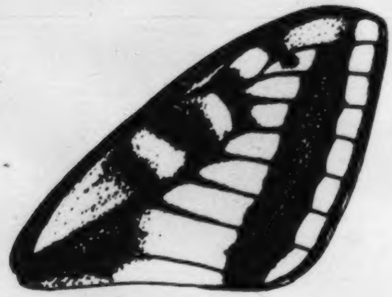
a. *P. m. aliaska*. Pink Mountain, British Columbia.

b. *P. m. dodi* yellow morph. Nacmine, Alberta.

c. *P. zelicaon X machaon* black morph. Bragg Creek, Alberta.

d. *P. zelicaon X machaon* black morph. Bragg Creek, Alberta.

e. *P. p. asterius*. Karlsruhe, North Dakota.



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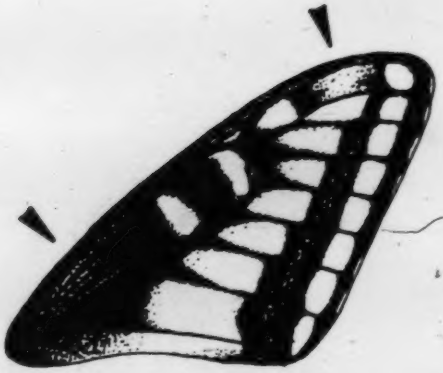

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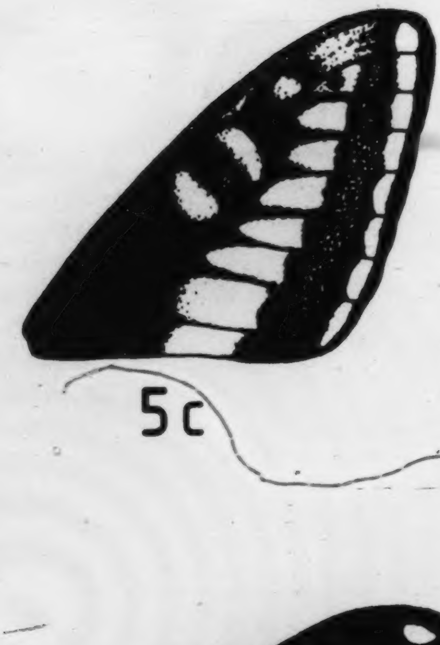

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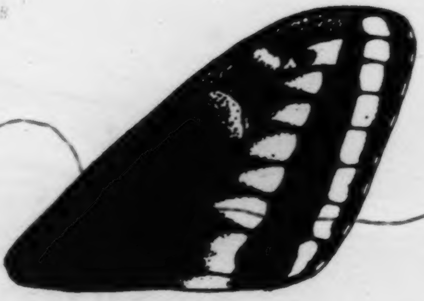

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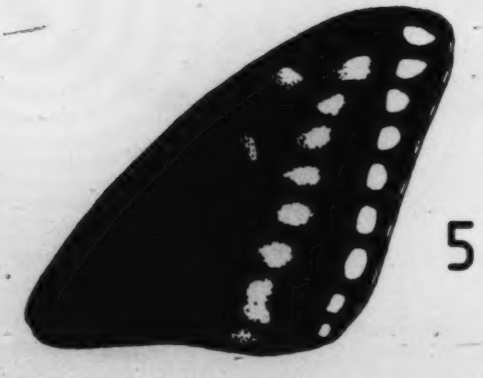


5e

Figure 6. Lateral view of thorax + abdomen. Wings and head have been removed.

a. *P. m. aliaska*. Pink Mountain, British Columbia.

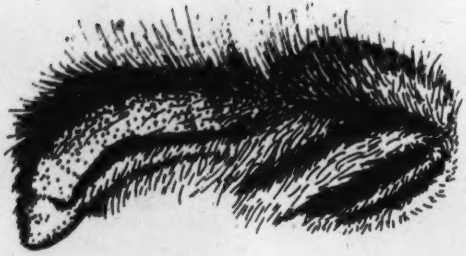
b. *P. m. dodi* yellow morph. Nacmine, Alberta.

c. *P. zelicaon* yellow morph. Wintering Hills, Alberta.

d. *P. zelicaon X machaon* yellow morph. Bragg Creek, Alberta.

e. *P. zelicaon X machaon* black morph. Bragg Creek, Alberta.

f. *P. p. asterius*. Karlsruhe, North Dakota.



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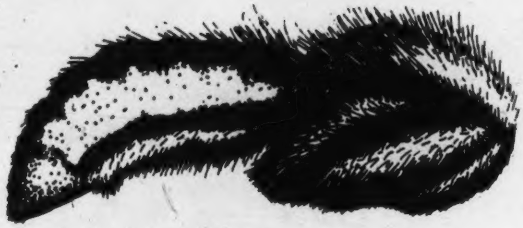

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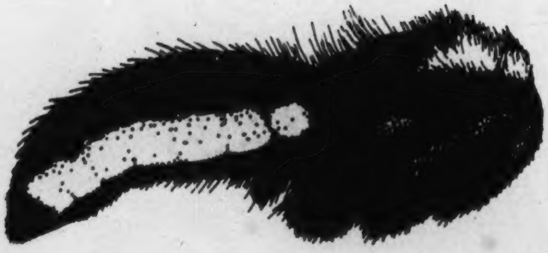

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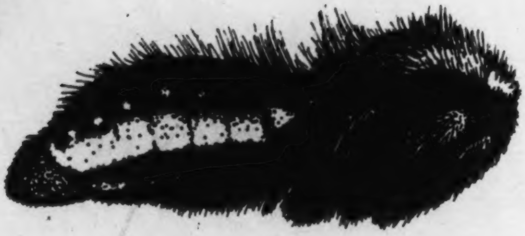

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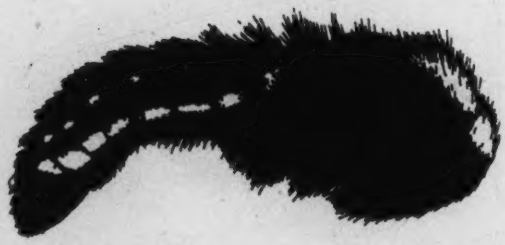
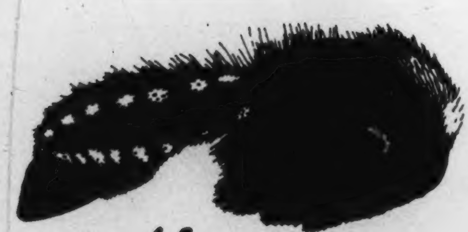


6e



6f

number of times I scored the presence of the black supergene, which is known to affect a number of adult color pattern characters.

Character states were defined on the basis of examination of a number of specimens from several different populations, to form natural transformation series of character states. For most characters, the state expressed in *P. m. aliaska* was arbitrarily assigned to the beginning of the series. Individuals were scored against both the written descriptions of character states and a number of standard specimens. Standard and illustrated specimens were labelled as such and have been deposited in the Strickland Museum, University of Alberta.

2.2.2 Electrophoretic characters

A total of 860 adult *Papilio machaon* group specimens were used in electrophoretic analyses. These were frozen live and maintained at -20 C, and most were homogenized within a few weeks of being frozen. However, bands were still readable if whole specimens were kept frozen for more than two years. For these specimens, 50% more homogenate than usual was used.

Tissue for electrophoresis was obtained by dissecting thoracic and abdominal contents from specimens which had been allowed to thaw on ice just before use. The specimen was grasped between thumb and forefinger and cut with small scissors along the length of the dorsum of the thorax and most of the abdomen. Abdominal contents, including most of the gut and anterior part of the reproductive system, were removed with tweezers and placed in a small glass mortar on ice. In females an effort was made to obtain the gut and only a few eggs in early development. The corpus bursa was not used. The specimen was then placed on a piece of balsa wood and the incision in the thorax braced open with pins. The thoracic contents, comprised almost entirely of flight muscle, were removed after they were cut away from the cuticle with fine pointed scissors. Freshly eclosed specimens were the most difficult to obtain thoracic tissue from, since the tissue usually still had a high fluid content.

After tissue had been removed for electrophoresis, specimens were pinned through one side of the thorax and mounted as regular taxonomic specimens. Since they were dried with the dorsal incision closed, close inspection is needed to see if a specimen was used for electrophoresis, although some specimens required gluing to prevent them from spinning on their pins. All specimens were given a unique number and labelled to allow the morphometric and electrophoretic character states to be associated for each individual.

Thoracic and abdominal tissue samples were homogenized separately, each in 0.2 ml homogenizing solution. Tissue was ground in two successive aliquotes of 0.1 ml, with a glass mortar and pestle. It was centrifuged at 7000 RPM for 5 minutes, and the amounts used for each type of stain are indicated in Table 3. Homogenate which was not used immediately in electrophoresis was frozen and stored at -20 C in the centrifuge tubes (culture tubes), and covered with Parafilm®. Most samples gave interpretable bands from frozen homogenate, though esterases and IDH deteriorated the most rapidly when subjected to successive freeze-thaw cycles. If care was taken not to disturb the precipitate on the bottom of the tubes, samples remained clear enough to use without being re-centrifuged.

The electrophoretic apparatus used was the same as that described by Rolseth and Gooding (1978), in whose laboratory and under whose direction I did the preliminary work for this study. Some changes have been made in their methods since publication. These include: 1) making the "B" solution with 25.6 ml of 1M H3PO4, 5.7 gm Tris and 0.46 ml TEMED, brought up to 100 ml with distilled water; 2) making the homogenizing buffer with 7.0 ml H20, 1.0 ml B, .300 gm polyvinylpyrolidine and 40 mg DL-dithiothreitol; 3) forming stacking gels with 20 slots; and 4) sealing the edges of the apparatus with parafilm rather than a plug gel. Also gels were run at pH 8.9 and pH 8.2, using 24 ml and 60 ml of 1M HCl, respectively, in the stock "A" solution. Tissue was electrophoresed at 40 miliamp/gel for 2.0 hours in pH 8.9 gels, and 3.5 hours in pH 8.2 gels.

After removal from the electrophoretic apparatus, gels were placed in a 8x17 cm plastic dish for staining. Gels

Table 3. Electrophoresis conditions and staining methods

Homogenate is measured in microliters.

Protein	EC no.	Gel %	Gel pH	Homogenate thorax	Homogenate abd.	Buffer	Stain	Cofactor	Substrate
aGPD	1.1.1.8	9.0	8.9	5	5	Tris pH 7.2, .05 M	NBT-PMS	NAD	25 mg alpha-glycerophosphate
G-6-PD	1.1.1.49	6.0	8.9	25-30	5-10	Tris ph 7.2, .05 M	NBT-PMS	NADP	10 mg glucose-6-phosphate
IDH	1.1.1.42	9.0	8.9	30	15-20	Tris pH 8.0, .05 M	NBT-PMS	NADP, MgCl2	20 mg DL-isocitrate
MDH	1.1.1.37	9.0	8.9	5	5	Tris pH 7.2, .05 M	NBT-PMS	NAD	20 mg L-malate
ME	1.1.1.40	4.5	8.2	15	30	Tris pH 7.2, .05 M	NBT-PMS	NADP, MgCl2	10 mg L-malate
ODH	1.1.1.73	9.0	8.9	50	30-50	Tris pH 7.2, .05 M	NBT-PMS	NAD.	10 drops octanol
APK	2.7.3.3	7.0	8.9	25	-	Tris pH 7.2, .05 M	NBT-PMS	NADP,ADP,HK, + MgCl2,G-6-PD	20 mg arginine phosphate
Esterases	3.1.1.2	7.0	8.9	30	-	phosphate pH 6.0,0.2 M	Fast Blue RR		30 mg alpha-naphthyl-acetate
General protein		7.0	8.9	20-25	-	3.5% perchloric acid	Coomassie Brilliant Blue G		

were covered by 30 ml staining solution and incubated at 30 C, except for the general protein stain and the initial buffer equilibration for esterases, which were performed at room temperature. Staining methods are summarized in Table 3, and except for the use of MgCl2 rather than MnCl2 as a cofactor for IDH, they are fairly standard applications of recipes available in Shaw and Prasad (1970) or Brewer (1970).

For esterase staining, gels were first placed in buffer for 10 minutes to reduce background staining. The substrate, which was dissolved in 3 ml acetone, was then added, and the gel incubated for 14 minutes before fresh substrate with stain was added. The two esterase loci used in this study showed much greater activity with alpha-naphthyl-acetate than with beta-naphthyl-acetate or AS-D-acetate, and were not significantly inhibited by eserine.

APK was generally stained with Coomassie blue, since it seemed to be the most common protein that could be resolved by this method in thoraces. The identity of the APK bands was ascertained in several homozygous individuals and the single individual (a male) with an allelic variant, using the staining technique of Gooding and Rolseth (1979). The general protein staining involved first fixing the gel in 7% acetic acid for 8 minutes, then placing the gel for 24 hours in 3% perchloric acid with Coomassie blue predissolved in it. Destaining, in 7% acetic acid, required about 24 hours.

When staining was complete, gels were fixed in 7% acetic acid overnight before being wrapped in Saran® wrap and stored. Most gels were read immediately after staining, and were still readable for at least two years if stored under cool, dark conditions.

An attempt was made to stain for a variety of other enzymes, using recipes of Brewer (1970), Shaw and Prasad (1970) and Menken (1980). These included ADH (with ethanol, isopropanol and sorbitol), AO (with benzaldehyde and heptaldehyde), GLUO, GDH, GA-3-PD, GlyDH, LDH, G6PDH, SDH, TO and XDH. In these attempts, bands were either very faint or did not appear. For esterases there were at least 3 loci higher than Est-4 on the gels, of which Est-1 (a monomer) appeared very faintly and there were at least two or more loci between Est-1 and Est-4 which overlapped each other and could not be consistently distinguished. Gels treated with the general protein stain showed a number of bands with at least some variation, but except for the loci used in this study, these did not appear in clear, consistent patterns.

My interpretations of the genetic basis for variation in a particular locus were dependent on satisfying a few simple conditions. Homogenate from an individual had to always produce bands after electrophoresis, and these bands had to conform to a limited number of discrete patterns within a population. Also it had to be possible to recheck band positions by re-running homogenate from two individuals beside each other.

Hypotheses of subunit composition of the protein molecules were based on the maximum number of bands produced by any one individual for a particular locus. If there were either one dark or two lighter bands for any one individual at a particular locus, then these were interpreted as, respectively, homozygous or heterozygous expressions of a monomeric protein. Most of the proteins stained were considered dimers, as evidenced by two light outer bands and a single darker inner band for heterozygotes. One enzyme (ME) produced 5 discrete bands in heterozygotes of two relatively distant alleles, and so may have been a tetramer. None of the loci included in this study, except possibly APK, were sex linked. Heterozygotes were present in both sexes for all other loci, including G-6-PD, which is frequently sex linked in other taxa.

The genetic inheritance of alleles was not checked through breeding experiments. However, environmental induction of particular alleles seems unlikely. Most of the local populations surveyed had allelic distributions that were at Hardy-Weinberg equilibrium proportions. Also it was quite possible for larvae obtained from different foodplants to have equivalent banding patterns. On the other hand, larvae and pupae which were kept under the same temperature and light regimes did not produce equivalent bands. When considered on a broader scale, the general distribution of allelles showed an excellent correspondence with morphometric, and ultimately taxonomic, characters.

In any event, my taxonomic conclusions are not strictly dependent on the correctness of my genetic interpretations of protein banding patterns. The bands are treated as equivalent to any other taxonomic character and are more discrete than the character states in my morphometric analysis. An additional advantage of the electrophoretic characters I used is that they probably represent a relatively unbiased selection of loci. The choice of loci for staining was influenced by my ability to consistently obtain bands and my ability to interpret variation in a consistent manner, both of which factors are independent of the morphometric characters measured.

2.2.3 Larval spots

In the course of the collection and rearing of *Papilio machaon* group larvae, I recorded the color of the spots on each individual. Spot color was determined by eye and by comparing larvae against each other. Though I did not consistently use a standard for comparison, I would estimate that there is at most one or two percent error in my assignment of larvae to either a yellow or an orange group. Yellow spotted larvae had a relatively uniform color, whereas orange spotted larvae varied somewhat more. I considered all the orange larvae as a single group, because I did not feel confident of my ability to consistently separate pale orange from bright orange larvae, as did Clarke and Sheppard (1955b), with the aid of a standard color atlas.

For almost all individuals, spot color was determined from fifth instar larvae. The exceptions were larvae which were late in the fourth instar and obviously belonged to one of the two groups. Questionable specimens were not scored until they were late in the fifth instar. Larvae from a particular locality were generally collected over an area of at least several hectares and were represented by several instars which were scored as they reached the fifth instar. Nonetheless some of the smaller samples probably contained a significant proportion of siblings, which would preclude much confidence in statistical tests for differences between small populations. All larvae reared from wild-collected females were considered separately from individuals collected in the larval stage.

I contacted several lepidopterists who had reared larvae in western Canada, and examined published records of spot color for the whole *P. machaon* group. Records and sources for the *P. machaon* group in North America are included in Table 19.

2.3 Numerical analyses

2.3.1 Principal components analysis

Principal components analysis (PCA) visualization of clusters in multivariate data, is relatively assumption-free, and provides a basis for internally consistent, simple comparisons of both individuals and populations. PCA seems to give fairly accurate representation of distances between data points, and has been used successfully in studies of hybrid swarms (Neff and Smith, 1979; Pimentel, 1981). Relatively few characters appear to be required to elucidate patterns of racial variation. Thorpe (1985) showed that patterns with 90% confidence could be obtained from as few as 8-10 characters in grass snakes in Europe. Also, it is easy to relate samples not used in the initial analysis to those that were, by applying factor loadings.

Three major PCAs were performed on an initial group of 728 specimens, almost all of which were from western Canada and particularly Alberta. These 728 were all the specimens I had available, in early 1984, for which I had complete scores for all the morphometric and electrophoretic characters considered in this study. An effort had been made prior to this to obtain a reasonably broad sampling of the different geographic populations and morphotypes known from the region, including those described by other authors. One PCA was performed on only the morphometric characters, one on only the electrophoretic characters and one on the combined morphometric and electrophoretic characters together. The same individuals were used in all three PCAs, to give a more meaningful basis for the comparison of character variation patterns. Then the factor loadings were applied to individuals which could only be completely scored for one of the two main character suites.

All work for this section of the study was carried out with the Midas statistical package on the mainframe Amdahl computer system at the University of Alberta. The principal component function was used only with the "unscaled" option in this package, to allow easier application of loadings to other specimens, and also to maintain a more direct relationship between raw data and resultant scores on the principal components axes. However, the 11 morphometric characters were scaled before use in the PCA, to make the range of variation equivalent for each of these charaters. Scaling factors and PCA loadings are indicated on Tables 16 and 17. Electrophoretic character scores were not scaled, since these were already recorded in a manner that gave equivalent weights to each character.

Electrophoretic characters were scored one allele at a time. Each allele known from my work on the *P. machaon* group was considered a character with three character states and scored: 1, if the allele was absent; 2, if it was present in combination with another allele for that locus; and 3, if it was present in the homozygous state. By this method, there were 42 electrophoretic characters, though only a small proportion of these were of significance to the scores on the first few principal component axes. If only 2 alleles were known for a locus, as in Est-4, these had a perfect negative correlation with each other, and in a sense were redundant. However, both character were retained to maintain consistent scoring of raw data. The APK locus was not used in the PCA, since with only one variant in 728 individuals, it would have been meaningless.

An alternative method for scoring electrophoretic characters is used in some numerical analyses (Mickevitch and Mitter, 1981; Buth, 1984). In this method, each locus is considered a character, and each allele is coded on the basis of its relative mobility. This method was rejected because it does not allow distinction between an individual homozygous for a particular allele, and an individual heterozygous for two alleles located an equal distance on either side of the homozygous allele.

2.3.2 Other statistics

Electrophoretic data were also analysed using the Biosys-1 package of Swofford and Selander (1981). Allele frequencies, heterozygosity indices and tests for Hardy-Weinberg proportions were calculated. All individuals with partial electrophoretic information were used, giving a total sample size of 860.

Hardy-Weinberg equilibrium measures provided tests of gene pool homogeneity, and complemented the multivariate clustering techniques. First, the entire sample for a region was tested as a whole before being divided into major groups which might be different species. If the subsets were much closer to equilibrium after the subdivision, this was considered evidence of a significant degree of gene flow within but not between the subgroups.

Discriminant function analysis (DFA) was applied to subgroups where PCAs did not give clear indications of the number of species in a region or the nature of distinctions between them. DFA was applied to reared adults obtained from southern and south-central Alberta, where adults from different major populations showed only slight separation into the major groups distinguished in other regions. Discriminations were based on the different foodplants, on which larvae were collected. DFA was also applied to the geographically separated subspecies of *P. machaon*, to give an assessment of the accuracy of identification of specimens.

2.4 Interpretation

2.4.1 Species concepts

The term species has been used by biologists in a variety of different ways. This lack of consistency of usage of the term has resulted in considerable confusion in its application to biological phenomena, and is responsible for serious breakdowns in communication among biologists. Because of this difficulty, I explain my species concept, and discuss the functional relationships of other species concepts. I apply it to sexually reproducing animals with no known fossil record.

The lack of total consistency of usage of the term species has not prevented systematists from sorting out species as they believe they see them in nature. In fact some, for example Blackwelder (1967), see this part of taxonomy as a sort of learned trade which cannot be precisely characterized or defined. The arrangement of specimens into convenient groups or kinds, called species, is dependent on a certain amount of practice, subject to correction by other taxonomists. In that sense there is a significant element of tacit community knowledge which regulates the actions of systematists. This is probably the basis for the oft-repeated aphorism that species are whatever a good taxonomist says they are.

The perpetuation of a tacit concept such as species involves modelling the interpretation of data from one series of organisms onto the interpretation that has been achieved by another person for another set of organisms. The neophyte systematist begins to aquire a sense of what comprises a species only after the completion of several such exercises. A species concept is thus a kind of primary concept. Understanding how to interpret certain kinds of information becomes a matter of developing a sense of similarity relations and applying it in a manner sanctioned by experienced peers. This part of taxonomic training thus involves the transfer between people of a conceptual paradigm, in the sense of Kuhn (1970).

These considerations do not mean that I view the application of species concepts as a predominantly subjective endeavor. For most species concepts several basic rules seem widely accepted. For example different individuals from one egg batch or litter are not diagnosed as belonging to different species. Also, any phenotype known to be due to unusual environmental or developmental conditions does not warrant placement in another species. And finally, if geographic variation in appearance or ecological characteristics is relatively continuous, then only a single species is indicated. Even if the criteria for species are not explicit, there is little doubt that most species names refer to meaningful divisions of the biological universe. The relatively good correspondence of folk classifications to scientific classifications (eg. Irving, 1953; Berlin, 1973; Hunn, 1975; Posey, 1983) constitutes some of the strongest support for the objective reality of species.

Since the uses of systematics are primarily scientific, there is a need to make its operations repeatable, quantifiable and testable. Since most systematists have acknowledged the fact that species tend to be clusters of like individuals, many of them have focussed on this aspect of species. Even workers whose main research objectives lie in the elucidation of evolutionary mechanisms may begin their discussion of species by referring to them as "discontinuous arrays" (Dobzhansky *et al* 1977:166). However, some systematists predominantly view species as phenetic covariance clusters, and de-emphasize any reference to reasons for the existence of these clusters. Examples include Ehrlich (1961), who identifies species as relatively arbitrary groups of organisms delineated by overall character similarity, or Nelson and Platnick (1981:12), who see species as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters". This view appears strongly influenced by the desire to make the process of distinguishing species as tractable as possible, particularly in terms of its mechanical simplicity.

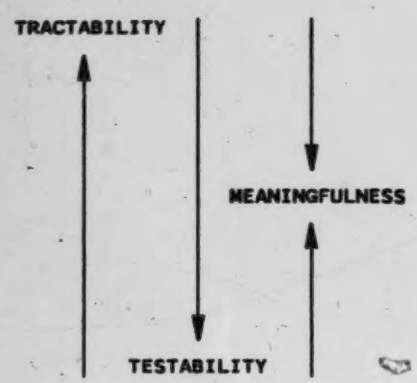
Other systematists may choose to emphasize the property which is perceived to maintain distinctions between species and unity within species. Interfecundity is seen as the character that makes such a group of organisms a biologically coherent entity, with an evolutionary integrity that is reflected by interspecific differences at a number of levels. A presently popular definition of this type is that of Mayr (1969), who defines species as "groups of interbreeding natural organisms that are reproductively isolated from other such groups".

Mayr's so-called biological species definition is an attractive formulation because hypothesized specific distinctions may be tested by the conceptually simple process of checking for hybrid sterility. However, it is often very difficult, if not impossible, to determine whether organisms may hybridize in nature. As well, species descriptions based on hybrid sterility are in some ways as arbitrary as species descriptions based on phenotypic clusters, since the degree of hybrid fertility which is accepted before a specific distinction is recognized is itself an arbitrary procedure. One way of dealing with the latter objection has been to characterize different populations as species only if they exhibit 100% hybrid sterility (eg. Key 1982). Unfortunately this definition is so restrictive that many organisms presently recognized as belonging to different species would have to be lumped together if the definition were rigorously applied.

The wish to make the process of sorting out species more objective thus seems to have led in two major directions (Table 4). Grouping on the basis of phenetic covariance appears to be a pattern-oriented approach which emphasizes tractability, while a greater reliance on interbreeding data implies a process-orientated approach which emphasizes hypothesis testing. Both of these directions can lead to the absurd extreme of operationalism, in which a definition is conceived as no more than a corresponding set of operations (Hull 1968).

The history of the sytematics of the *P. machaon* group provides examples of both kinds of operationalism. W.H. Edwards' names are an example of far greater emphasis on morphotypes than hybridization information. This is particularly noticeable in his treatment of the *P. machaon*

Table 4. Functional relationships of major species concepts



Species Concepts	Examples in *P. machaon* group
1. *Kinds* - primary concept defined by use.	
2. Phenetic clusters; smallest samples with unique characters.	Edwards (1895) Remington (1968a)
3. *Evolutionary species* - single lineage maintaining its own evolutionary identity.	
4. *Biological species* - interbreeding natural population, reproductively isolated.	Ferris & Emmel (1982)
5. Populations between which any hybrids are 100% infertile.	Hagen (1882)

populations in the western United States, upon which he bestowed four specific epithets despite knowing that the forms the names referred to were probably all part of the same extended gene pool. Part of the problem is that the species concept Edwards claimed to follow seemed to encorporate both genetic continuity and phenetic homogeneity, while the way in which he actually applied his species names almost exclusively reflected phenetic homogeneity and covariance.

Hagen's (1882) review of the western United States members of the *P. machaon* group was published during the same period as Edwards' work, but showed the opposite tendency to that of Edwards. He looked for and found specimens with character states and combinations that were intermediate between those attributed to all the previously described forms. He concluded that all the North American species of the *machaon* group (excluding *P. indra*) should be be considered as local or climatic varieties of *P. machaon*. Hagen may well have found a number of specimens which were hybrids between *P. machaon* and *P. zelicaon*, but did not concern himself with the proportion of the total population which his phenetically intermediate specimens represented. His taxonomic conclusions were made less meaningful by his overly strict adherence to the interbreeding criterion of his species concept, and hence he fell into the same trap of operationalism that reduced the value of Edwards' work.

The main fault of operationalism is that it emphasizes practicability in the application of a definition, but restricts the flexibility and generality of the definition in a way that reduces its meaningfulness. This is because definitions function as convienient phrases whose purpose is to remind one of the basic elements of a concept. Concepts, on the other hand, imply a reference to something which happens insides one's head. The definitions we use to explain or apply a concept are not a complete expression of that concept.

Species concepts can be viewed as a balance between practicability and meaningfulness. Definitions may be applied strictly, but they may not distinguish groups of particular relevance. Alternatively, if a species concept is particularly vague or difficult to apply in practical situations, then its potential meaningfulness is of little use. Both practicability and meaningfulness should be assessed in terms of the reason for naming species, which is the identification of organisms in a way that allows the user of the name to efficiently communicate information about their relationships with other organisms.

In some taxa, such as the *P. machaon* group, species concepts can be applied only relatively loosely. As in most taxonomic work, there is a need to distinguish variation at the level of local populations, geographic races and species. Numerical methods were used in a predominantly descriptive manner. Geographic patterns of variation were first examined within major character suites, such as structural and electrophoretic characters, and then compared among suites. Finally, these patterns of variation were interpreted in terms of species concepts, especially through inferences of gene flow and the maintainance of identity in time and space.

2.4.2 Subspecies concepts

The recognition of subspecies is a relatively arbitrary aspect of taxonomy. Subspecies limits are far more difficult to set than are species limits, which are generally determined by interbreeding criteria, or even higher taxa, for which monophyly has become the most important criterion. In some taxa subspecies names do serve a useful function, but such names are greatly overused and abused in butterfly taxonomy. Nonetheless, I believe that consistently applied subspecies names have a place in zoological nomenclature. This opinion seems to be shared by most systematists who work on relatively well known groups (such as birds -Wiens, 1982).

My main criterion for formally recognizing a differentiated series of populations or an ecological race as a subspecies is that three quarters or more of the specimens (*cf* Mayr 1969) can be distinguished without the aid of locality labels. However, for some taxonomically borderline populations, I retain the use of long established names to communicate more effectively and also to compare the results of my study with those of other work. If this study were concerned with more obscure organisms, rather than with a group of high-profile and perennially popular butterflies, I would have little compunction in abandoning use of some of the subspecies names which I employ.

Subspecies are preeminently geographic divisions of species. Situations for which subspecies names are most appropriate involve major allopatric and easily identified sections of a species. Subspecies should be at least parapatric, with intermediates occurring along only a relatively narrow zone. Phenetic homogeneity within a subspecies should be quite high compared to that within zones of intergradation. Examples of disjunct and relatively distinct populations can be found in *P. indra* (eg. Emmel and Emmel, 1967).

Although most subspecies have been described on the basis of structural characters, ecological characters may also be important. In particular, sharp clines or disjunctions in use of larval foodplant suggest that genetic distinctions may be involved and a subspecies designation may be appropriate, if the populations are geographically separate. For example, the geographically abrupt shift in larval foodplants between *Papilio glaucus glaucus* Linneaus and *P. glaucus canadensis* Rothschild and Jordan has now been shown to be related to differences in abilities to use these foodplants and in diapause characteristics, as well as adult size and color pattern (Scriber, 1982 and 1984). Hence ecological distictions between populations can be important to taxonomists as indicators of major genetic distinctions.

Local populations often show close adaptation to local ecological conditions (eg. Endler 1982). Comparisons between such populations may also show shifts in the mean values of a variety of morphometric characters. Unfortunately many subspecies are named on the basis of population samples from accessible areas even though it is highly likely that these populations are relatively continuous in less accessible intervening regions. Such a practice gives the impression of relatively discrete subspecific variation, when in reality the few characters that the subspecific names are based on are much more clinal. In my study I concentrate on describing the patterns of variation within *P. machaon* group species. The main reason for using subspecies names at all is to relate my own findings to previous work, much of which has been couched in terms of description of new specific and subspecific taxa.

2.4.3 Taxonomic conventions

It is no easy task to fit patterns of variation in the *Papilio machaon* group to a standard system of nomenclature. The main difficulty in classifying populations and individuals of the *P. machaon* group from western Canada is that in some regions groups of individuals seem like genetically distinct entities in sympatry, while in other areas extensive hybridization is indicated.

In zoological taxonomy, hybrids are usually dealt with either by simply noting them as rare occurrences, or using them to as evidence of genetic continuity between two populations. Extended populations, which interbreed in some regions but not others, are generally described as a single species with a circle of races, or subspecies. More complex situations, such as those identified in the *P. machaon* group, appear to be rare in animals (but see Ehrlich 1961, on butterflies).

The International Code of Zoological Nomenclature does not provide rules for hybrid names. Hybrid populations seem to be more commonly encountered in botanical work, where they may be referred to as hybrid swarms. For this reason, I follow the practice of the International Code of Botanical Nomenclature (1983), and more general guides in taxonomy such as Schenk and McMasters (1956), in constructing hybrid names. Unfortunately, the convention of ordering the parental names by the sexes which contributed to the hybrid swarms is not useful to naming hybrid populations of the *P. machaon* group. I place the specific epithets of the parental species, with an "X" between them, in order of dominance in the mean hybrid phenotype.

I prefer to use form names as little as possible in taxonomic treatments, mainly because I feel they have a very limited communication value. As well, form names are not recognized in the International Code of Zoological Nomenclature, and this has led to a considerable uneveness of usage (eg. Scott, 1981). A better alternative for many taxa would be to name the determining genes and alleles, rather than phenotypes of uncertain consistency and derivation. This practice is commonly followed by workers on well known taxa such as *Drosophila* and *Peromyscus*, species of which have been the subject of a great deal of basic genetic research. The *P. machaon* group is not as well understood genetically, though important steps have been made by Clarke and Sheppard in the 1950's. Gene names would allow the application of the same term to characteristics in different species. A good candidate for such treatment is the adult morph with black wings, whose features are almost certainly determined by homologous alleles in different populations of *P. polyxenes*, *P. zelicaon* and *P. machaon*. In *P. zelicaon* the effects of this gene have been referred to by some authors as the form *nitra*, while the gene contributes to much of the typical form of *P. p. asterius* and *P. m. bairdii*. The black wing allele is closely linked with but not the same as the allele for yellow abdominal spots. This is indicated by the rare occurrence of the form *hollandi*, which has black morph wings but a yellow lateral stripe on the abdomen. This situation is analogous to that described by Clarke, *et al* (1968) in *Papilio memnon*, whose genes controlling wing pattern, body color and tail length are closely linked.

I feel that a genetically oriented view of polymorphism and hybridization will greatly help to further understanding of the often complex population interactions within the *P. machaon* group. For this reason, I tend to refer to alleles and individuals in the following sections, rather than to forms and types.

3. CLASSIFICATION AND RECOGNITION OF TAXA

In a scientific publication, the presentation of conclusions normally succeeds the presentation of results. However, the taxonomic conclusions of the present study will be presented before the supporting data. This is because I am proposing several changes to the systems of names which have previously been applied to the *Papilio machaon* group. In order to simplify the presentation of data in succeeding sections, my system is summarized in the present section. Detailed reviews of holomorphological and ecological features of the included taxa follow. These are discussed in the final sections, which deal with evolutionary hypotheses.

3.1 Summary of Taxonomic Assignments

The following list is based on Miller and Brown (1981), and summarizes the disposition of all the taxonomic names applying to the *P. machaon* group in western Canada and Alaska. It includes all names with type localities in the study area, as well as names applying to populations which are found, or have at some time been considered to have been found, in the study area.

P. machaon Linneaus, 1758:462. Type locality(TL)-Sweden.

a. *P. m. aliaska* S.H. Scudder, 1869:407. TL-Nulato, Alaska.

=*joannisi* R. Verity, 1907:pl.10, fig.17. TL-Nulato, Alaska.

=*petersii* A.H. Clark, 1932:8-9. TL-Kuyukok River, Alaska.

b. *P. m. bairdii* W.H. Edwards, 1869:200. TL-"Arizona", restricted to Fort Whipple, Arizona, by Brown(1975). =*brucei* W.H. Edwards, 1895:239. TL-"Colorado", restricted to Glenwood Springs, Colorado, by Brown (1975).

c. *P. m. oregonius* W.H. Edwards, 1876:208. TL-near The Dalles, Oregon (neotype locality is at Hepner, Oregon [Brown, 1975]).

d. *P. m. hudsonianus* A.H. Clark, 1932:6-7. TL-Kettle Rapids, Manitoba.

e. *P. m. dodi* J. McDunnough, 1939:216-217. TL-Red Deer River, 50 miles N. E. of Gleichen, Alberta (probably near Dorothy [Kondla, 1981]).

f. *P. m. pikei* F.A.H. Sperling, 1986. NEW SUBSPECIES. TL-Dunvegan, Alberta.

P. zelicaon Lucas, 1852:136. TL-"California".

=*nitra* W.H. Edwards, 1883:162-163. TL-Judith Mts., Montana.

=*gothica* C.L. Remington, 1968:2-5. TL-Gothic, Colorado.

=ab. *mcdunnoughi* J.D. Gunder, 1928:162. TL-Waterton Lakes, Alberta.

P. zelicaon X machaon NEW HYBRID MORPH

P. polyxenes Fabricius, 1775:444. TL-"America", restricted to Cuba by Rothschild and Jordan (1906).

a. *P. p. asterius* Stoll, 1782:194. TL-New York, Virginia and Carolina.

P. machaon X polyxenes NEW HYBRID MORPH

=*avinoffi* F.H. and R.L. Chermock, 1937:11-12.

TL-Whirlpool River, Riding Mts., Manitoba.

P. polyxenes X machaon NEW HYBRID MORPH

=*kahli* F.H. and R.L. Chermock, 1937:12-13. TL-Riding Mts., Manitoba.

3.2 Description of *Papilio machaon pikei*

Of the five major sections of *P. machaon* known from western Canada, four were described many years ago. The fifth occurs exclusively within the Peace River region, and appears to have been collected once (Llewellyn Jones, 1951) before being rediscovered by E.M. Pike and me in 1980. The Peace River race of *P. machaon* is ecologically very distinct from *P. m. aliaska* and *P. m. hudsonianus*, and is geographically disjunct from *P. m. dodi* and *P. m. oregonius*. Although it is very similar in holomorphological features to the other subspecies of *P. machaon* in western Canada, it is as different from each of these as they are from each other. In order to facilitate discussion about the evolution of this race, it is described below. All measurements are based on the specimens used in the principal components analyses, listed in Table 16.

Papilio machaon pikei, new subspecies

Adult (not figured). **Male.** Mean forewing length 40.8 mm (range 36.5-47.0). Dorsal hindwing with yellow scales covering proximal portion of wing almost to base, except in cell Cu2, in which yellow scales are confined to postmedian region. Black pupil of dorsal hindwing eyespot along lower edge of red scales and connected to margin of wing. Pupil club-shaped or a narrow line. Blue and red scales of eyespot separated by few or no black scales. Basal half of ventral forewing disc covered by yellow scales. Postmedian area of ventral hindwing of most specimens with distinct patch of orange scales in two or fewer cells. Thorax covered by long yellow hairs ventral to wings. Ventral side of abdomen with yellow hairs on all segments. Broad yellow lateral band on abdomen, covering claspers. Subdorsal spots above lateral abdominal band very rare. **Female.** Like male, but larger (mean forewing length = 42.6 mm, range = 39.5-45.5), and with more rounded wing.

Immatures. Eggs, larvae and pupae very similar in all stages to those of *P. m. oregonius* (see Perkins *et al*, 1968 for photographs) and to *P. m. dodi*. Fifth instar larvae with segmental spots orange or yellow, but most individuals with orange spots. Background color of mature larvae from flat blue-green to bright emerald green. Pupae either mottled brown or green, but not a mixture of brown and green as in some specimens of *P. m. aliaska*. Larval foodplant *Artemisia dracunculus*, on warm, dry, eroding exposures.

Type series. Holotype: male. Canada, Alberta; Dunvegan (s. Fairview); June 14, 1981; F.A.H. Sperling; [on dry, grassy, south-facing slopes above Peace River] (CNC).

Allotype: female. same data as for holotype. (CNC).

Paratypes. Abbreviations: E4# = F.A.H. Sperling electrophoresis number, *Ad* = *Artemisia dracunculus*, f = female, m = male. All reared specimens have pupal shell and some have fifth instar larval skin attached to card below specimen. Pupation and emergence dates are omitted in the following list. There will be 78 paratypes deposited in public institutions, and 20 remain in the personal collection of E.M. Pike.

2f, 6m: Canada, B.C.; Attachie; larva coll. Aug 9 '81; F. Sperling; on *Ad*; e4# 521-526,528,529 [all emg. 1983], (CNC). **2f, 1m:** Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. Aug. 9, 1981; on *Ad*; [all emg. 1982]; F. Sperling (CNC). **1m:** Attachie, British Columbia; 35 km W. Ft. St. John; larva coll. July 9, 1981; on *Ad*; F. Sperling (CNC). **1m:** Taylor, B.C.; July 3 '80; F. Sperling (CNC). **1f:** larva on *Ad* at Taylor, B.C. on Aug. 18, 1980; [emg. 1981]; F.A.H. Sperling; e4# 627, (CNC). **1f:** Canada, B.C.; Taylor; larva coll. July 8 '82; F. Sperling; on *Ad*; e4# 439 (CNC). **3f, 6m:** Canada, B.C.; Taylor; June 21, 1982; F. Sperling; including e4# 6,7,55,56,59,124,128,395; (BCPM: e4# 59[f],124[m]. AMNH: e4# 6[m],55[f]. USNM: e4# 56[m], 128[f]. remainder to CNC). **1f, 2m:** Canada, B.C.; Taylor; July 8, 1982; F. Sperling; e4# 10,31,140; (CNC: e4# 31[m]. BM: e4# 10[m],140[f]). **2f:** Clayhurst Ferry, B.C.; larva on *Ad*; Aug. 17 '80; emg. 1981; F.A.H. Sperling; including e4# 117; (CNC: e4# 117[f]. AME: 1f). **3m:** Clayhurst Ferry, British Columbia;

larva coll. Aug. 9, 1981; on *Ad*; emg. 1982[2] & 1983[1]; F.A.H. Sperling; including e4# 519, (CNC). 4f, 7m: Canada, B.C.; Clayhurst Ferry; larva coll. Aug. 16 '82; F. Sperling; on *Ad*; emg. 1983; e4# 504,507,508,511-513,515-518,520, (AME: e4# 507[m]. remainder to CNC). 5m: Alberta, 5 km NW Highland Park; June 14, 1981; F. Sperling; e4# 115,116,676,678,679, (CNC). 5m: Canada, Alberta; Highland Park; 35 km w Fairview; June 9, 1982; F.A.H. Sperling; e4# 41,42,43,44,45, (APME: e4# 41,43. CNC: e4# 42,44,45). 9m: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 12, 1982; Ted Pike, (CNC). 5m: Canada, Alberta; Highland Park; 20 mi. W. Fairview; June 13, 1982; Ted Pike, (Pike). 1m: Dunvegan, Alberta; larva on *Ad*; Aug. 16, 1980; emg. 1981; F.A.H. Sperling, (CNC). 1f, 2m: Alberta, Dunvegan; June 14, 1981. T. Pike, (Pike). 1f: Canada, Alberta; Dunvegan; larva coll. Aug. 15, 1982; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 438, (CNC). 1f, 3m: Canada, Alberta; Dunvegan; June 22, 1982; F.A.H. Sperling; e4# 142,150,546,547, (CNC: e4# 142[m], 547[m]. UASM: e4# 150[m],546[f]). 1f: Dunvegan, Alta.; 30 VI 85; coll. by E.M. Pike; (Pike). 1m: EX OVA; Dunvegan, Alta.; 18 VI 85; coll. by E.M. Pike; (Pike). 4m: 10 mi. S.E. Fairview; Alberta; 17 June 1981; coll. by E.M. Pike; (Pike). 2m: 10 mi. S.E. Fairview; Alberta; 20 & 22 June 1981; coll. by E.M. Pike; (Pike). 1f, 2m: Canada, Alberta; 10 mi. S.E. Fairview; June 22, 1982; Ted Pike; (Pike). 1f: 10 mi. S.E. Fairview; Alta., 20 VI 85; coll. by E.M. Pike, (Pike). 1m: Canada, Alberta; Peace R. area, Camp Island; 22 mi. E. Dunvegan; F.A.H.

Sperling; larva on *Ad* on Aug. 15, 1980; [emg. 1981], (CNC). 1f: larva on *Ad*; at Peace R. (town), Alberta; on Aug. 15, 1980; emg. 1981; F.A.H. Sperling; e4# 625, (CNC). 4m: Alberta, Peace River (town); June 10, 1981; F. Sperling (CNC). 2m: Canada, Alberta; Peace River (town); June 13, 1981; F.A.H. Sperling; e4# 114,681, (CNC). 1m: Canada, Alberta; Kleskun Hills; 25 km n.e. Grande Prairie; June 19, 1982; F.A.H. Sperling; e4# 394, (CNC). 1f: Canada, Alberta; Kleskun Hills; e. Grande Prairie; larva coll. Aug. 12 '81; F.A.H. Sperling; on *Ad*; emg. 1983; e4# 437, (CNC).

Derivation of specific epithet. It is a pleasure to name this subspecies after E.M.(Ted) Pike, who has resided in the Peace River region from 1979 to 1985, and has given me much help over the last 15 years.

Distinguishing features. Adults of *P. m. pikei* resemble those of *P. m. oregonius* in general maculation and size, but can usually be distinguished by the more rounded forewings and more narrow, connected eyespot. *P. m. aliaska* adults resemble those of *P. m. pikei* strongly in maculation, but are separated by larval foodplant, preference for alpine habitat, and smaller size (mean forewing length = 37.5 mm for males, 40.3 mm for females). Though the range of *P. m. pikei* extends in isolated populations to within 25 km of *P. m. aliaska*, at Hudson Hope, there is no evidence of any increased similarity of these two subspecies in the area. *P. m. hudsonianus* adults are separated by preference for boreal forest habitats and a much higher frequency of subdorsal abdominal spots. *P. m. dodi* is easily distinguished from *P. m. pikei* by the greater amount of black scales and hairs, especially on the ventral forewing disc and ventral side of the thorax. Approximately 75% of individuals of *P. m. pikei* can be correctly distinguished from those of other subspecies of *P. machaon*. Features which distinguish this subspecies within *P. machaon* are discussed at greater length in the following chapters.

P. m. pikei has the same larval foodplant as the southern subspecies of *P. machaon*, but shares several morphometric and electrophoretic similarities with the northern subspecies. For these reasons, as well as its geographic range, *P. m. pikei* is important in illustrating the previously unrecognized link between these taxa.

Range. *P. m. pikei* is composed of a series of populations along approximately 500 km of the Peace River, in northeastern British Columbia and northwestern Alberta. It also occurs at the Kleskun Hills badlands, northeast of Grande Prairie, Alberta. The range of *P. m. pikei* may have once extended farther westward along the Peace River. A specimen at the University of British Columbia collection, which is labelled "Findlay, B.C.", may be from Findlay Forks, 110 km west of Hudson Hope. However there is little likelihood that any populations have continued to survive along this part of the Peace River, since it was flooded to form Williston Lake in the late 1960's.

3.3 Key to Adults of *P. machaon* Group in Western Canada

The following key was devised to assist in the identification of museum specimens. For this reason, no electrophoretic characters were used. However, since some taxonomic distinctions depend on habitat information, this has been used also. The key is a guide, and not a substitute for extensive field experience or long comparative series.

1. Black scales on disc of DHW restricted to basal half (Fig.2); side of abdomen with a broad, yellow, longitudinal band and in some specimens with rounded spots above it (Figs.6a-d)...............2.

1'. Black scales extended over more than half of DHW disc (Fig.3); side of abdomen with only a series of square or rounded segmental yellow spots (Figs.6e-f)...................................9.

2.(1') *All of the following character states*: Black pupil in anal region of DHW connected to margin (Figs.1a-b,2,3); yellow scales covering most of VFW disc (Fig.5a); yellow hairs extended around ventral part of metathorax (Fig.6a); yellow scales extended over more than 80% of male claspers(Fig.6a).
Or no more than one of the following: Anal pupil unconnected to margin but flattened and at bottom of red area (Fig.1c); yellow scales in VFW disc restricted to thick yellow streaks or general flush extended over more than quarter of disc (Fig.4b);

yellow scales extended over only 50-80% of male claspers (Fig.6b) ....*P.machaon* Linneaus 4.

2.' Not as above ....3.

3.(2') *All of the following*: Anal pupil round and centered in red area (Fig.1d); red and blue areas of anal eyespot more than 3/4 separated by black scales (Figs. 1b,1d,2,3); disc of VFW with at most few thin streaks or light sprinkling of yellow scales (Figs.5c-e); metathorax with yellow hairs from both sides not in contact ventrally (Figs.6b-d); without distinct yellow spots above lateral abdominal band (Figs.6b-c); less than 50% of male claspers covered by yellow scales (Figs.6c-d)

Or no more than one of the following: Anal pupil large, round and centered if connected to margin (Fig.2) or small and oval at bottom of red area if unconnected (Fig.1c); red and blue areas of anal eyespot separated between 1/4 and 3/4 of full width by black scales (Fig.1c); disc of VFW with thick streaks of yellow or a general flush over less than 1/4 of the disc (Fig.5b); some distinct yellow spots above lateral abdominal band (Fig.6c); yellow scales over 50-80% of male claspers (Fig.6b).......
.................................*P. zelicaon* Lucas

3'. Not as above: most specimens with club-shaped pupil connected to margin; also most specimens with two or more of character states intermediate between extremes of *P. machaon* and *P. zelicaon* as defined above, rather than combination of extreme states..7.

4.(2) Found near dry grasslands or eroded clay banks in hot habitats; large (FW length usually 40 mm or more); forewing apices pointed or not, with distal margin convex or concave; most specimens with yellow scaling of DHW anal cell Cu2 extended close to or beyond divergence of veins Cu1 and Cu2 (Fig.2: character states 2-4); few specimens with abdomen with spots above lateral band............5.

4'. Found in forested boreal regions or on alpine tundra in cool habitats; smaller (FW length usually less than 40 mm in males); forewing apices of most specimens rounded, with convex outer margin (Fig.5a); yellow scaling of DHW anal cell Cu2 in most specimens restricted to distal 1/4 (Fig.2: character state 1); abdomen with or without yellow spots above lateral band ....6.

5. Found in the southern and central B.C. Interior, during April to September; anal pupil of eyespot connected to margin in most specimens, but club-shaped rather than a flat line; separation between blue and red areas of anal eyespot variable; with a substantial amount of orange in 2 or more cells of the VHW postmedian band; most specimens with forewings pointed, with a concave

distal margin; (Note: a few summer generation *P. m. dodi* from the southern Alberta and Saskatchewan prairies will key out here) ....*P. machaon oregonius* (Edwards)

5.' Found in Peace River region of northeastern B.C. and northwestern Alberta, during June and early July; anal pupil of many specimens flat rather than club shaped; most specimens with very little black separation between red and blue in anal eyespot; most specimens with substantial amounts of orange in only one or no cell of the VHW postmedian band; forewings pointed or rounded ....*P. machaon pikei* Sperling

6.(4') Found in Alaska, Yukon, western Northwest Territories, and northern British Columbia, most specimens on alpine tundra; DHW anal pupil in shape of thin line, at bottom of red area, and connected to margin (Fig.1a); red and blue areas of anal eyespot with no or very little black separation (Fig.1a); no spots or in few specimens one or two spots on abdomen above lateral band ....*P. machaon aliaska* Scudder

6'. Found in boreal forest from Alberta to northern Quebec; DHW anal pupil in most specimens club shaped; red and blue areas of anal eyespot separated or not by black scales; at least one yellow spot above lateral abdominal band in most specimens ....*P. machaon hudsonianus* Clark

7.(3') Found near dry grassland or eroding clay banks in hot prairie habitats of southern Alberta or Saskatchewan; anal pupil of DHW club-shaped and connected to margin; forewing apex of many specmens pointed, with concave distal margin; hindwing tails often long, slightly narrowed in middle and curved (Fig.2); yellow scales in DHW anal cell Cu2 may extend beyond divergence of veins Cu1 and Cu2 (Fig.2: character states 3-4); no distinctly separated yellow spots above lateral abdominal band ....*P. machaon dodi* McDunnough

7'. Found in broad range of habitats, but most in southern zones of boreal forest; anal pupil of DHW varied; forewing apex of most specimens rounded, and distal margin straight or rounded; hindwing tails of medium or short length, straight and not constricted in middle (Fig.3); yellow scales of distal hindwing cell Cu2 in most specimens restricted to distal quarter; less than five yellow spots above lateral abdominal band ....yellow morph hybrids 8.

8.(7') Found in Manitoba or eastern Saskatchewan *and* one or more of the following charcter states present: anal pupil on DHW round and centered; disc of VFW with at most light sprinkling or thin streaks of yellow scales; thorax with yellow hair not meeting ventrally and no yellow hairs on ventral midline of first two abdominal segments; male claspers covered over less than 50% of surface by yellow scales..... ....*P. machaon X polyxenes*

8'. Found in western Saskatchewan and westward, with any of the following combinations:

A. Found in predominantly forested habitats and with club shaped, connected pupil.

or B. Specimen with between two and five of the following six character states: 1, DHW anal pupil connected to margin or unconnected, flattened and at bottom of red area; 2, Blue and red areas of anal eyespot not separated by black along at least 1/4 of boundary; 3, disc of VFW with yellow scales or thick streaks over at least 1/4 of area; 4, metathorax with yellow hair meeting ventrally; 5, one to five distinct spots above lateral abdominal band; 6, yellow scales over more than 50% of male claspers ....*P. zelicaon X machaon*

9.(1') Found in southern and central Manitoba or southeastern Saskatchewan; postmedian band of VHW with substantial amounts of orange in at least two and, in most specimens all , cells; distinct yellow spots in two subdorsal rows on at least 5 and usually all segments of abdomen.................10.

9'. Found in southwestern Saskatchewan and south or central Alberta; postmedian band of VHW with substantial amounts of orange in less than six cells (only two or three in most specimens); distinct yellow spots in subdorsal position on abdomen usually absent on at least 2 segments...... ....11.

10.(9) Anal pupil of DHW unconnected to margin or club shaped if connected; blue and red areas of anal eyespot fully separated by a band of black scales; less than half of hairs on tegula yellow; yellow scales in apical cell of postmedian band of VFW variable; postmedian band of VHW with orange in all eight cells; lower half of side of abdomen with rounded yellow spot on each abdominal segment; yellow spots in subdorsal position on abdomen absent on no more than two segments; less than 10% of male claspers covered by yellow scales; females with greatly reduced postmedian band on DHW, compared to males ....*P. polyxenes asterius* (Stoll)

10'. *All three of the following character states*: anal pupil club-shaped and connected to margin; more than 50% of hairs on tegula yellow; apical cell of VFW postmedian band with distinct patch of yellow, but occupying less than half of cell area; *or one or more of the following character states*: anal pupil a thin line at lower edge of red area, connected to margin; blue and red-areas of anal eyespot partly or completely unseparated by black scales; apical cell of VFW postmedian band more than 50% covered by yellow scales; postmedian band of VHW with no orange in at least one cell; large square spots or broad band of yellow along lower half of abdomen; yellow spots in subdorsal position on abdomen absent on at least three segments; more than 10% of male claspers covered by yellow scales; females with postmedian band on DHW the same width as on males..................*P. polyxenes X machaon*

11.(9') Anal pupil of DHW round and centered in red area; blue and red areas of anal eyespot fully separated by black scales; male claspers with less than 10% yellow scales ....
........................black morph of *P. zelicaon*

11'. One or more of the following character states: anal pupil of DHW connected to margin or low and oval if unconnected; blue and red areas of anal eyespot of DHW not separated by black scales along at least 1/4 of boundary; male claspers with more than 10% yellow scales...................................12

12.(11') Found near dry grassland or eroding clay banks in hot prairie habitats.............................
.....................black morph of *P. machaon dodi*

12'. Found in predominantly forested habitats ....
...............black morph of *P. zelicaon X machaon*

4. MORPHOMETRIC AND ELECTROPHORETIC CHARACTERS

4.1 Characters of Adults

4.1.1 Introduction

Only a few species within the *Papilio machaon* group are easy to distinguish on the basis of morphometric characters. The most divergent of these is *P. alexanor* Esper, which has a striped wing pattern unlike the other species of the group, but shares with them an apotypic larval color pattern and larval foodplant.

The remaining species in the *P. machaon* group are much more similar to each other with respect to adult holomorphology. Only *P. indra*, whose males have an unusually long tooth row on the valvae of the genitalia, and *P. hospiton* Géné whose males have an unusually short tooth row, have diagnostic interspecific distinctions in genitalia. There is appreciable intraspecific genitalic variation in the remaining five of the eight species in the group, but this occurs even within local populations (unpublished data). Female genitalia have not been investigated in the same detail as those of males, probably because these seem to show even less diagnostic utility. Structural differences, other than those in genitalia or wing shape, have not been reported for the *P. machaon* group.

Chromosomal variation has not shown much taxonomic utility. Maeki and Remington (1960) reported that *P.*

polyxenes specimens had an extra "m" chromosome. However, *P. machaon* populations exhibited considerable variation in the number of supernumery chromosomes (Maeki 1976). For example, *P. machaon* in Japan had from one to four supernumery chromosomes, which were for the most part indistinguishable from the remaining chromosomes. Clarke *et al* (1977) showed some difference in the form of the Y chromosome between *P. polyxenes* from the eastern United States and *P. machaon* from Finland. They also reported the heteropyknotic body of males to be useful markers in hybridization studies. Chromosomal characters have not been used in the present study, largely because of the substantial difficulty involved in obtaining good preparations.

To my knowledge, there have been no reports about enzyme allele variation in the *P. machaon* group. The technique of gel electrophoresis has proven to have considerable utility in elucidating sytematic relationships in many other taxa, including butterflies (Berlocher 1984, Buth 1984). These methods have been modified in the present study for use with the *P. machaon* group.

Wing and body color pattern, and wing shape, have been the main morphometric characters used to distinguish among *P. machaon* group species. For identifications of *P. machaon*, *P. zelicaon* and *P. polyxenes*, no one character is completely dependable, and most diagnoses list several characters. However, there has been no effort to rigorously quantify these differences using multivariate techniques.

For the separation of *P. zelicaon* from *P. machaon* (including *P. m. bairdii*, *P. m. oregonius* and *P. m. dodi*), the characters noted by Edwards (1883) are used the most. He cited, in particular, the shape of the pupil of the anal eyespot, the amount of yellow scaling in the cell of the ventral forewing, and the amount of yellow hair on the thorax and abdomen. *P. zelicaon* adults are distinguished on the basis of the rounded and centered pupil, and the lesser amount of yellow on the body and wings. Additional taxonomic characters include the forewing apical angle, which is considered to be more pointed in *P. machaon* in many regions. Ever since Edwards (1893), the foodplant and habitat differences between these two species have been a major factor cited to support species status for these taxa where they overlap. Although some of the southern subspecies of *P. machaon* have at various times been considered as separate species, the unity of all the *A. dracunculus*-feeding populations has recently been recognized by Fisher (1980).

The main source of confusion between *P. machaon* and *P. zelicaon* has been the yellow morph populations in Colorado and east of the Rocky Mountains into Canada. In these regions, *P. machaon* adults are darker and the two species are much more easily confused (Fisher, 1980). This is particularly true of the spring brood of *P. machaon dodi*, which Hooper (1973) mistakenly listed as "*P. machaon* ssp." separately from his entry for the summer brood "*P. machaon brucei*" (R.R. Hooper, *in litt.* 1980). As well, there is a possibility of gene introgression from *P. machaon* into *P. zelicaon*. Many of the character states cited by Remington (1968a) to separate his *P. gothica* from Californian *P. zelicaon* tended toward those in "*P. brucei*" (*P. m. bairdii*) from Colorado.

Separation of *P. machaon* adults from those of *P. polyxenes* has also proved problematical. In the southwestern United States *P. m. bairdii* has a high proportion of individuals with a black color morph very similar to that of *P. p. asterius*. The two taxa have foodplant and habitat differences similar to those which distinguish *P. machaon* and *P. zelicaon*. Color pattern differences between black morph *P. machaon* and *P. polyxenes* are analogous to those between yellow morph *P. machaon* and *P. zelicaon*, in that *P. polyxenes* individuals tend to have less yellow scaling and a more centered anal pupil (Fisher, 1980). Also, *P. polyxenes* tends to have more orange scaling on the ventral hindwing. The black morph of *P. machaon* is reported to be very uncommon north of Colorado (Emmel 1975), and has not been reported previously from Canada.

In western Arizona and southeastern California, the differences between *P. machaon* and *P. polyxenes* are reversed relative to the differences between *P. p. asterias* and *P. m. dodi* or *P. m. hudsonianus*. In this region *P. p. coloro* is predominantly represented by yellow morph adults which are very similar to *P. zelicaon*. *P. m. bairdii*, on the other hand, is almost fixed for the black morph gene.

P. m. hudsonianus and *P. p. asterius* have caused taxonomic difficulties in Manitoba, where two local forms have received names. *P. m. avinoffi* is a yellow form which was distingushed from *P. m. hudsonianus* partly on the basis of a darker wing pattern, and the names were considered synonomous soon after the former taxon was described. The black morph *P. kahli* referred to black morph adults, and proved to be more taxonomically durable, probably because the form appeared to be distinguished by more differences in wing pattern. Most individuals were separated on the basis of more yellow on the wings and tegulae, as well as a less centered anal pupil (Hooper, 1973). In this way the form was similar to the dark morph of *P. m. bairdii*. However, it showed much more similar foodplant habits to those of *P. p. asterius* and did not have the same degree of reduction of hindwing orange. An additional feature used to distinguish *P. kahli* was the greater similarity of the female and male color pattern than in *P. p. asterias*.

The black adult form of *P. zelicaon*, which is relatively common east of the Rockies, has been considered by some authors to be a separate species, named *Papilio nitra*. Fisher (1977) showed that in Colorado the black form is a simple genetic variant of the more common yellow *P. zelicaon*. Its genetic control is basically the same as that of the color pattern of hybrids between *P. polyxenes* and *P. machaon* (Clarke and Sheppard, 1955b). Although most *P. zelicaon* and *P. polyxenes* adults are easily distinguished from each other on the basis of the yellow versus black adult color morph, the gene for the black color morph has introgressed some distance into *P. zelicaon* in the western part of its range. Most black morphs of *P. zelicaon* are distinguished from adults of *P. p. asterius* in Colorado on the basis of less orange on the ventral hindwings, slightly more yellow on the forewings, and fewer yellow spots on the abdomen (Fisher 1977, 1980). These differences are not considered fully reliable, and Fisher (1980, p. 184) described the forms as "confusingly similar". Only relatively subtle ecological distinctions separate the species.

The character states traditionally used by systematists to distinguish among *P. machaon*, *P. zelicaon* and *P. polyxenes* are especially difficult to employ, because the variation in color pattern in any one species is paralleled by the other species in other areas. Also, virtually no character states stand on their own, without consideration in a probabilistic sense or in combination with other characters. For this reason, I use multivariate statistical methods to provide more reliability in clustering groups of similar individuals, both at the level of populations and species. As well, two character suites were surveyed and compared with each other. One of these was the traditionally employed color pattern data, and the second was the new information about enzyme alleles.

4.1.2 Cluster resolution with principal components analysis

Principal components analyses (PCAs) were performed three times on the same original 728 individuals. One analysis was on morphometric data alone, a second on electrophoretic data alone, and the third on both combined. The PCAs of both electrophoretic and morphometric characters, whether separately or together, gave generally similar orientations of locality samples (Figures 7-8).

These samples were then compared with samples from or near the type localities of named populations, which were scored with the factor loadings derived from the analysis on morphometric data alone (Figure 9). From this comparison, it was clear that in all three principal components analyses the first axis separated most yellow morph populations of *Papilio machaon* (No. 1,2,3,5,12,13,15) from *Papilio zelicaon* (No. 8,9,10,16,17a,18,19), the second axis separated *Papilio polyxenes* (No. 11,17b,20) from the previous two groups and the third axis provided a partial separation of the *P. machaon* cluster. Figures 7 to 9 are a representation of selected populations on the first three principal component axes of PCAs on either morphometric or electrophoretic data alone. Factor loadings for all three PCAs are included on Tables 17 and 18. A list of the specimens used to derive the original PC loadings are included in Table 16.

Electrophoretic characters showed a close association between *P. m. dodi* (Figure 7, No. 15) and other *P. machaon* subspecies, while morphometric characters (Figure 8 and 9)

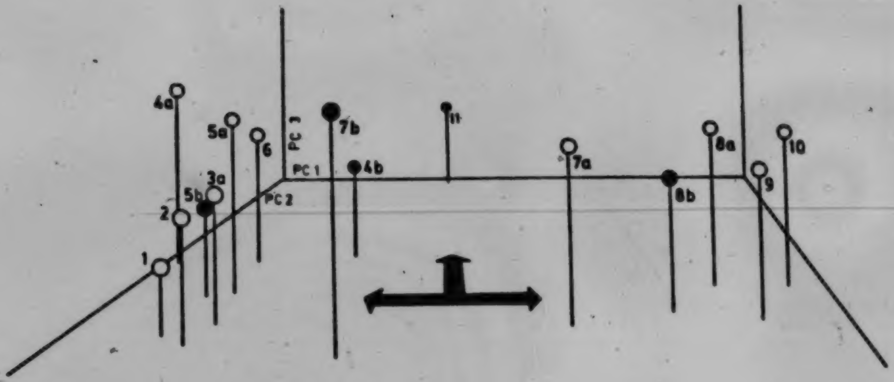
Figures 7 to 9. Representative populations plotted on first three principal component axes. See Table 5 for key to locations. Black circles indicate black morph adults, and empty circles indicate yellow morph adults. PC 1, PC 2 and PC 3 refer to the first, second and third principal component axes.

Figure 7. 3D.PCA on electrophoretic data alone. Populations include only individuals used in the original analysis.

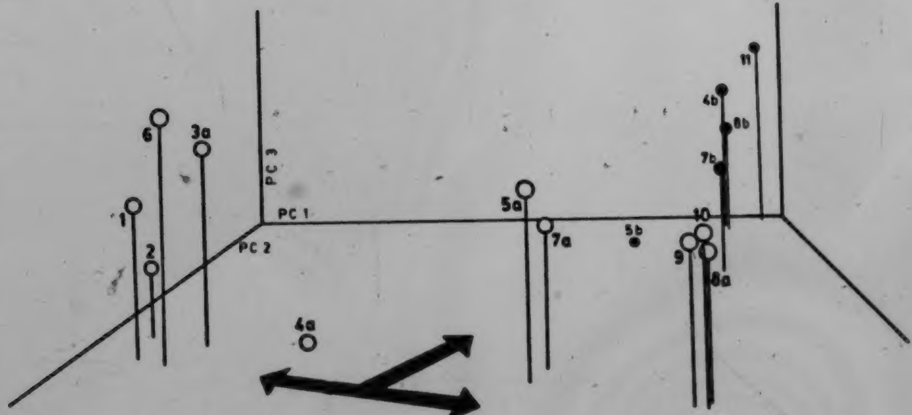
Figure 8. 3D.PCA on morphometric data alone. Populations include only individuals used in the original analysis.

Figure 9. Additional samples scored with morphometric loadings. Populations are partly or completely composed of individuals not included in original analysis, but scored with factor loadings from PCA on morphometric data alone. Most populations are either topotypic or from close to type localities.

7


4a
5a
6
3a
5b
2
1
PC 3
PC 1
PC 2
7b
4b
11
7a
8b
8a
9
10

8


6
3a
1
2
PC 3
PC 1
PC 2
4a
5a
7a
5b
11
4b
8b
7b
10
9
8a

9

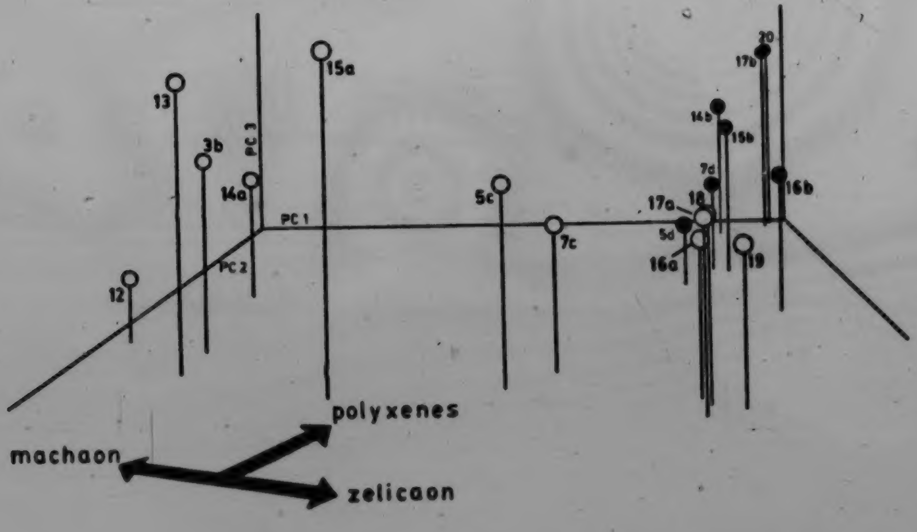

13
3b
14a
12
PC 3
PC 1
PC 2
15a
5c
7c
20
17b
14b
15b
7d
16b
18
17a
5d
16a
19
polyxenes
machaon
zelicaon

Table 5. Population samples plotted on Figures 7 to 9.

Letter after taxon name indicates yellow color morph (Y) or black color morph (B).

No. in figs.	Locality and region	Sample Size	Taxon and color morph
1.	Clayhurst Fy., Peace R. area, British Columbia	20	*P. m. pikei*
2.	Pink Mt., northern British Columbia	36	*P. m. aliaska*
3a.	Thompson, northern Manitoba	37	*P. m. hudsonianus*
3b.	Thompson, northern Manitoba	46	*P. m. hudsonianus* (expanded sample)
4a.	Duck Mt. Park, central Manitoba	1	*P. machaon X polyxenes* -Y
4b.	Duck Mt. Park, central Manitoba	7	*P. polyxenes X machaon* -B
5a.	Drumheller, southern Alberta	79	*P. m. dodi* -Y
5b.	Drumheller, southern Alberta	2	*P. m. dodi* -B
5c.	Drumheller, southern Alberta	105	*P. m. dodi* -Y (expanded sample)
5d.	Drumheller, southern Alberta	3	*P. m. dodi* -B (expanded sample)
6.	Kamloops, southern British Columbia	48	*P. m. oregonius*
7a.	Bragg Creek, south-central Alberta	65	*P. zelicaon X machaon* -Y
7b.	Bragg Creek, south-central Alberta	7	*P. zelicaon X machaon* -B
7c.	Bragg Creek, south-central Alberta	160	*P. zelicaon X machaon* -Y (expanded sample)
7d.	Bragg Creek, south-central Alberta	44	*P. zelicaon X machaon* -B (expanded sample)
8a.	Wintering Hills - West, southern Alberta	17	*P. zelicaon* -Y
8b.	Wintering Hills - West, southern Alberta	3	*P. zelicaon* -B
9.	Thunder Mt., northern British Columbia	23	*P. zelicaon*
10.	Vancouver area, southern British Columbia	10	*P. zelicaon*
11.	Caledonia, southern Wisconsin	15	*P. p. asterius*
12.	Steese Hwy., central Alaska	39	*P. m. aliaska*
13.	The Dalles area, northern Oregon	8	*P. m. oregonius*
14a.	Riding Mt. Park, central Manitoba	33	*P. m. hudsonianus* and *P. polyxenes X machaon* -Y
14b.	Riding Mt. Park, central Manitoba	32	*P. p. asterius* and *P. polyxenes X machaon* -B
15a.	Salida Co., southern Colorado	9	*P. m. bairdii*-Y
15b.	Salida Co., southern Colorado	17	*P. m. bairdii*-B
16a.	Judith Mts., central Montana	10	*P. zelicaon* -Y
16b.	Judith Mts., central Montana	8	*P. zelicaon* -B
17a.	Jefferson Co., northern Colorado	19	*P. zelicaon* -Y
17b.	Jefferson Co., northern Colorado	24	*P. p. asterius* -B
18.	Gothic, central Colorado	25	*P. zelicaon* -Y
19.	San Francisco area, central California	27	*P. zelicaon*
20.	Ottawa to Point Pelee, Ontario	59	*P. p. asterius*

indicated a more intermediate position for *P. m. dodi* between *P. zelicaon* and other *P. machaon* subspecies. Populations from the Alberta foothills, such as from Bragg Creek, were intermediate in both electrophoretic and morphometric characters. *P. m. oregonius* populations, which are not associated with *P. machaon* in most current publications, showed a close association with *P. machaon* on the basis of both character suites.

Although the second axis of each of the three PCAs served to separate *P. polyxenes* from both *P. machaon* and *P. zelicaon*, the black morphs associated with populations of predominantly yellow individuals were placed in an intermediate position between them in those analyses which included morphometric data. Electrophoretic characters showed a much closer association between the black and yellow morphs of most populations. The sample size from central Manitoba (No. 14) was relatively small, but nonetheless the single yellow morph specimen showed a close association with *P. machaon* for both character types. The black samples from central Manitoba showed a somewhat closer association with *P. machaon* than with *P. polyxenes* on the basis of electrophoretic characters, and grouped closely with *P. polyxenes* in morphometric characters.

Although plotting entire population samples on the principal component axes served to group most of these with either *P. machaon*, *P. zelicaon* or *P. polyxenes*, the associations of a number of intermediate samples were uncertain. In particular, this exercise did not distinguish between samples which were intermediate because the whole population was intermediate, and samples which contained a mixture of individuals of more than one of the above species. To facilitate such a distinction, the scores of all the individuals within a region or at a locality were plotted as frequency histograms on principal component axes. Since there seemed to be regional trends with respect to the frequency of intermediate individuals, the total sample used in the original PCAs was divided into five major regions, as shown by Figure 10. The frequency histograms on the first and second principal component axes of all three PCAs are shown on Figures 12 and 13.

Both morphometric and electrophoretic characters provided a good separation of *P. machaon* from *P. zelicaon* in southern and central British Columbia, as well as in the Peace River region. The few specimens which were intermediate on the basis of either character type grouped with *P. zelicaon* when both character types were considered together. The sample from southern Alberta and Saskatchewan showed a reasonable degree of clustering on the basis of electrophoretic but not morphometric characters, and the low frequency section between these two clusters was shifted toward *P. zelicaon* when both character suites were considered simultaneously.

When samples from the southern Alberta and Saskatchewan region were considered separately, it was clear that the

Figures 10 to 11.

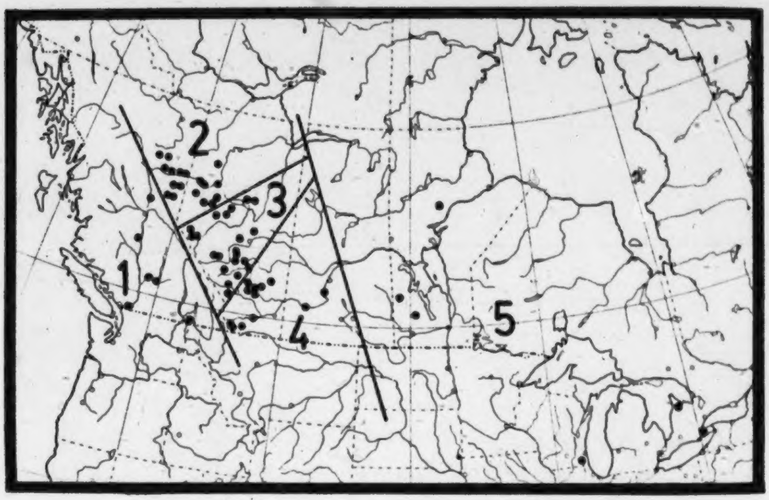
Figure 10. Western Canada, showing 5 major regions.

1. southern and central British Columbia
2. Peace River region
3. central Alberta
4. southern Alberta and Saskatchewan
5. Manitoba and eastward

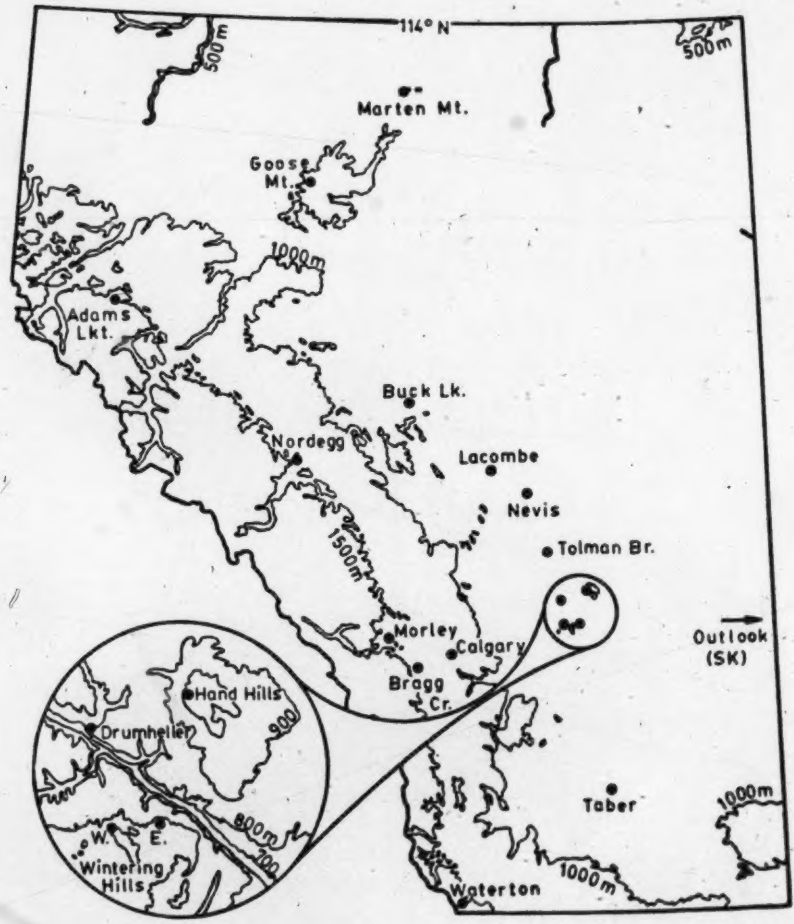
Dots show localities from which specimens were used in the initial PCAs.

Figure 11. Central and southern Alberta, with major localities. Localities refer to those used in figures 14 and 15.

10


2
3
1
4
5

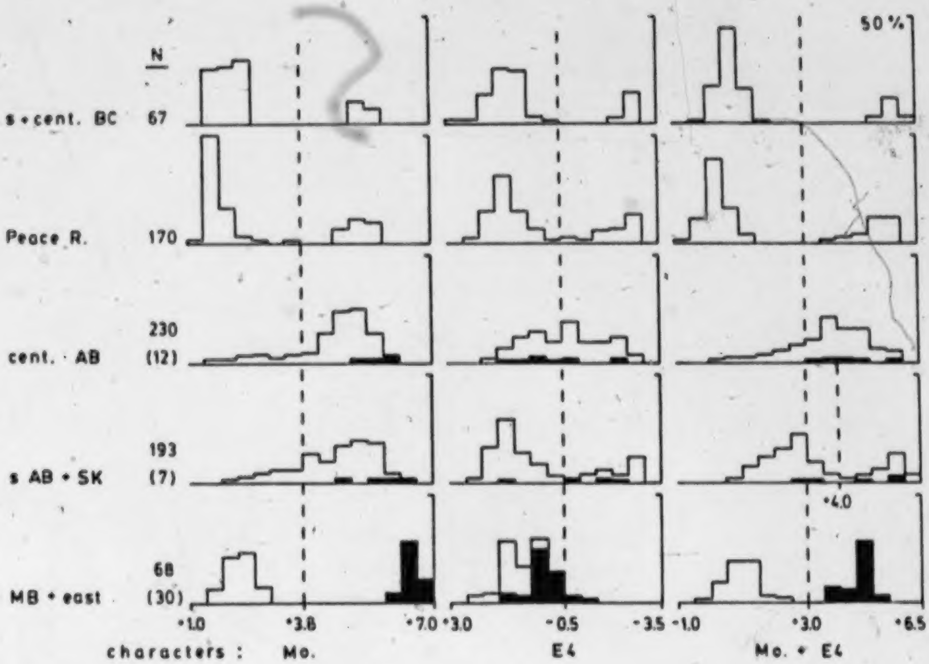
11


114° N
500 m
500m
Marten Mt.
Goose Mt.
1000m
Adams Lkt.
Buck Lk.
Nordegg
Lacombe
Nevis
1500m
Tolman Br.
Morley
Calgary
Outlook (SK)
Bragg Cr.
Hand Hills
Drumheller
900
800m
700
W.
E.
Wintering Hills
Taber
1000m
1000m
Waterton

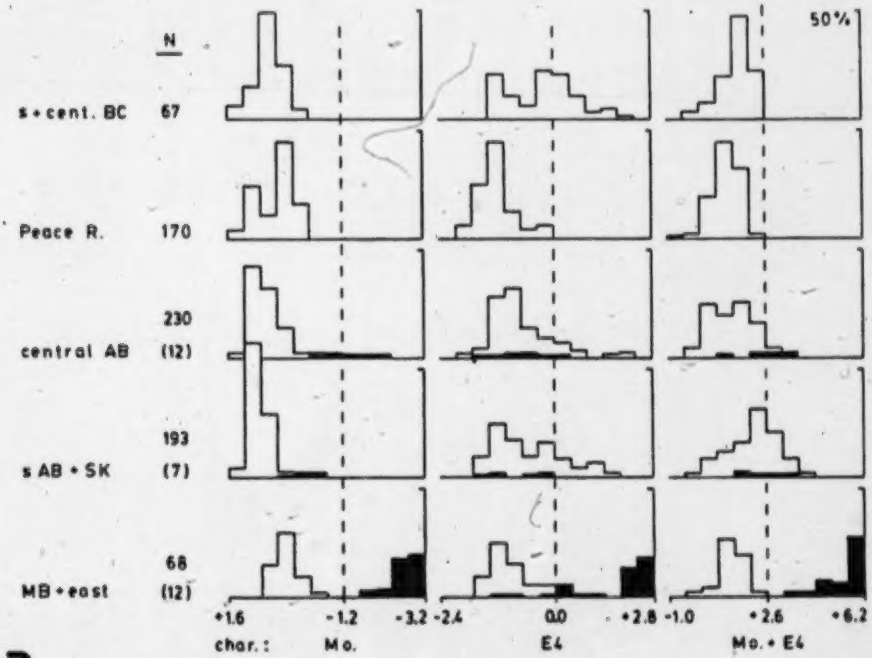
Figures 12 to 13. Component axes of three separate PCAs, with frequency histograms of all individuals in each of five major geographic regions (Figure 10): 1= s + cent. BC, 2= Peace R., 3= cent. AB, 4= s AB + SK, 5= MB + east. Only specimens used in original PCAs are included. Darkened portions of histograms indicate black morphs. Dashed lines indicate divisions between taxa, as referred to in text and Figure 22. Mo. = morphometic characters. E4 = electrophoretic characters.

Figure 12. First component axes, by major region.

Figure 13. Second component axes, by major region.


50%
N
s + cent. BC
67
Peace R.
170
cent. AB
230
(12)
s AB + SK
193
(7)
MB + east
68
(30)
+4.0
+1.0
+3.8
+7.0
+3.0
-0.5
-3.5
-1.0
+3.0
+6.5
characters :
Mo.
E4
Mo. + E4

12


50%
N
s + cent. BC
67
Peace R.
170
central AB
230
(12)
s AB + SK
193
(7)
MB + east
68
(12)
+1.6
-1.2
-3.2
-2.4
0.0
+2.8
-1.0
+2.6
+6.2
char. :
Mo.
E4
Mo. + E4

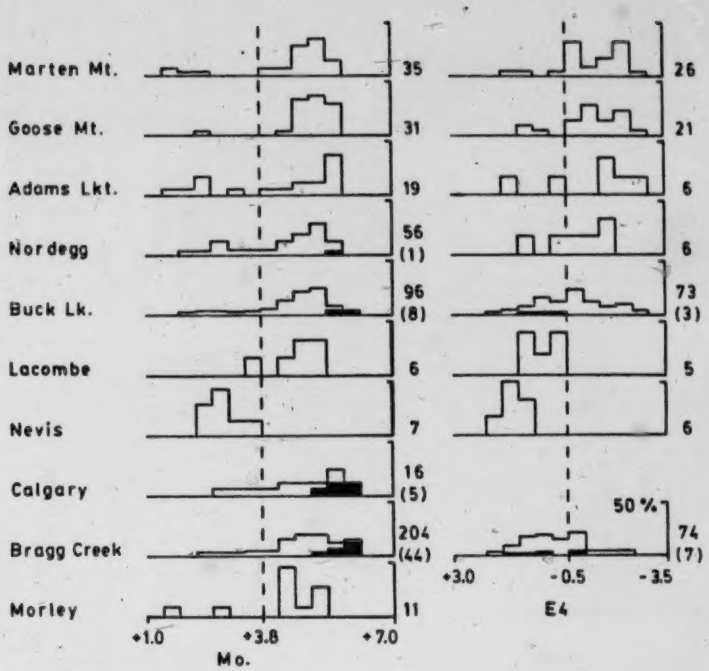
13

Figures 14 to 15. Locality samples plotted on first component axes. Some samples include individuals not used in original PCAs. Darkened parts of histograms indicate black morphs. Dashed lines indicate divisions between taxa, as referred to in text and Figure 22. Mo. = morphometric characters. E4 = electrophoretic characters.

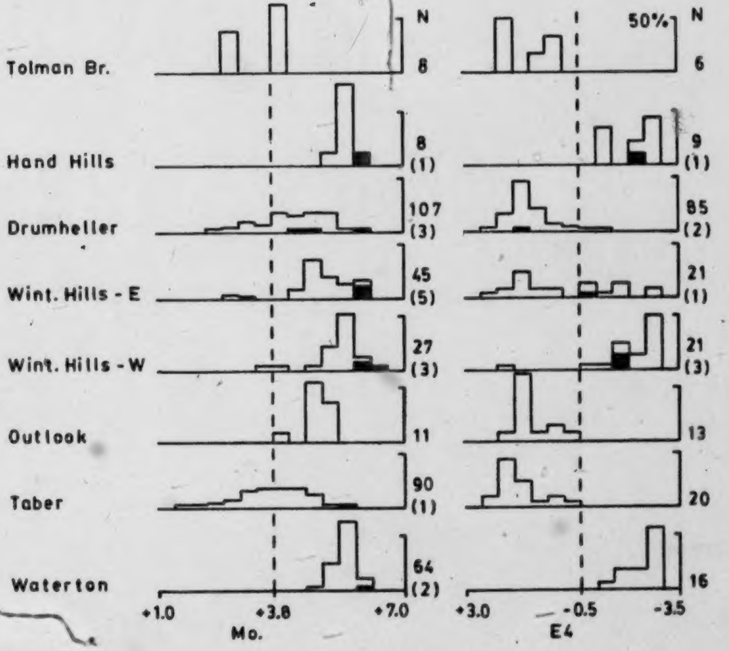
Figure 14. Central Alberta samples plotted on PC.1.

Figure 15. Southern Alberta and Saskatchewan samples on PC.1.

14


Marten Mt.
35
26
Goose Mt.
31
21
Adams Lkt.
19
6
Nordegg
56
(1)
6
Buck Lk.
96
(8)
73
(3)
Lacombe
6
5
Nevis
7
6
Calgary
16
(5)
50 %
Bragg Creek
204
(44)
74
(7)
Morley
11
+1.0
+3.8
+7.0
Mo.
+3.0
-0.5
-3.5
E4

15


N
50%
N
Tolman Br.
8
6
Hand Hills
8
(1)
9
(1)
Drumheller
107
(3)
85
(2)
Wint. Hills - E
45
(5)
21
(1)
Wint. Hills - W
27
(3)
21
(3)
Outlook
11
13
Taber
90
(1)
20
Waterton
64
(2)
16
+1.0
+3.8
+7.0
Mo.
+3.0
-0.5
-3.5
E4

frequencies of *P. machaon* and *P. zelicaon* differed greatly by locality (see Figure 15). Specimens collected along high river banks were likely to be more similar to *P. machaon* from other regions, especially in electrophoretic characters. Specimens from prairie hilltops were more likely to belong to *P. zelicaon*. This situation was well illustrated by the locality samples from the Drumheller region (for locations see Figure 11). The sample from the river bank just above the town of Drumheller contained only *P. m. dodi* and a few intermediate specimens. There were mostly just *P. zelicaon* in the samples from the Hand Hills and the western part of the Wintering Hills, which are about 15 and 12 km, respectively, from the nearest deeply cut river valleys or ravines. There was a mixture of both species at a hilltop on the eastern part of the Wintering Hills, which is about 4 km from the nearest deep ravine and 6 km from the banks of the Red Deer River.

This pattern was basically the same as that found in southern British Columbia, where *P. m. oregonius* is found in the dry grassland habitats of the central Interior, while *P. zelicaon* is far more common in forested and wetter habitats. In the Peace River region *P. m. pikei* also tended to be found on the dry river banks and *P. zelicaon* on the hills farther away from the river. However, an added complication here is that another subspecies, *P. m. aliaska*, frequents the boreal and especially the alpine regions of northern British Columbia, north of the Peace River.

In the predominantly forested regions of central Alberta, there seemed to be a different sort of relationship between *P. machaon* and *P. zelicaon* (Figure 14). At the northern localities (Marten Mt. to Adams Lkt.) there was a predominance of electrophoretic and morphometric character combinations which tended to resemble *P. zelicaon*, as well as a significant proportion of more intermediate individuals. There was, however, a relatively small number of individuals indistinguishable from northern *P. machaon*, even when the two character types were considered together, and it was unclear whether these formed a distinctive group from the others. In the more southerly localities (Buck Lk. to Bragg Cr.), the different phenotypes evident in the north tended to merge even more. Populations from single localities were composed of a few individuals indistinguishable from either *P. machaon* or *P. zelicaon*, but the majority were intermediate. There was a single peak near the midpoint between the two extremes, which tapered off smoothly to either side. The different phenotypes all occurred within the same habitat as well.

The most *P. machaon*-like individuals from the southern foothills of Alberta had morphometric character combinations more similar to *P. m. hudsonianus* than to *P. m. dodi*. In fact, no specimens were collected on the southern prairies which were as *P. m. hudsonianus* or *P. m. aliaska*-like as a few individuals which were taken at Bragg Creek and Buck Lake, at localities which are geographically close to *P. m.*

dodi populations. This suggests that the hybrid populations are at least partly a product of hybridization between *P. zelicaon* and the more northerly *P. machaon* races, rather than with *P. m. dodi*. On the other hand, most of the specimens from these two localities tended to be very similar to *P. m. dodi* in morphometric characters, while most were more intermediate between *P. zelicaon* and *P. machaon* in electrophoretic characters. This suggests that the very similar wing and body color pattern combinations which occur in both *P. m. dodi* and the hybrid swarms may have arisen in different ways.

In Alberta, the black wing color morph occurred together with the more common yellow members of both *P. machaon* and *P. zelicaon*. These specimens had a range of electrophoretic character combinations matching the remainder of the population they occurred with. This applied to individuals collected with other *P. zelicaon* specimens on prairie hilltops, the intermediate hybrid populations of the Alberta foothills, and the *P. m. dodi* collected along dry river banks. On this basis it appears as though this morph has become a regular part of all of these populations. Although the black morph in many respects resembles *P. p. asterius*, there was no good electrophoretic evidence of hybridization with *P. polyxenes* in these populations.

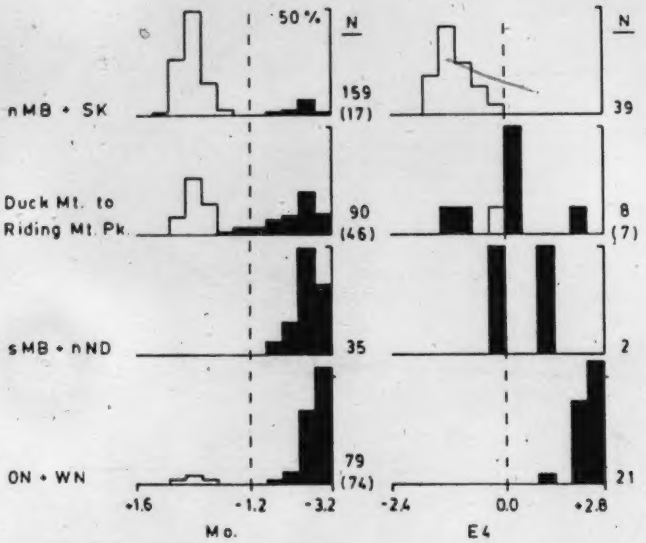
The situation in Manitoba was far less clear (Figure 16), though there probably are hybrid swarm populations in this region as well. These hybrid populations appear to be

Figures 16 to 17. Dashed lines indicate divisions between taxa, as referred to in text and Figure 22. Mo.= morphometric characters. E4 = electrophoretic characters.

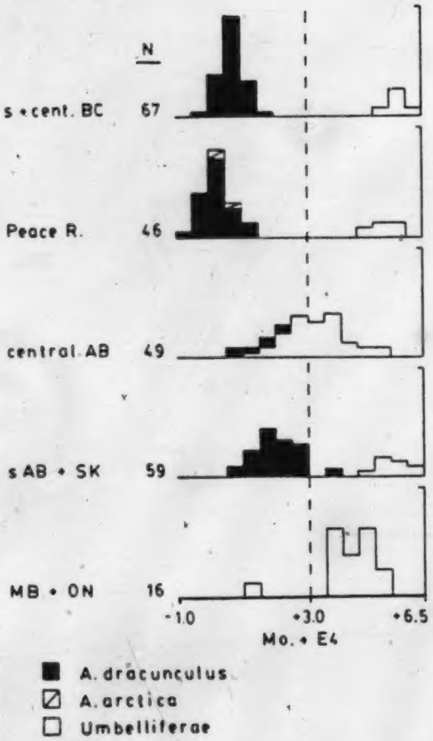
Figure 16. Area samples from Manitoba and eastward. Samples are plotted on second component axes, and some include individuals not included in original PCAs. Black morph individuals are indicated by darkened portions of histograms. Geographic areas: 1. nMB + SK = northern Manitoba and northern Saskatchewan, 2. Duck Mountain and Riding Mountain Parks, 3. sMB + nND = southern Manitoba and northern North Dakota, 4. ON + WN = Ontario and Wisconsin.

Figure 17. Adults reared from wild-collected larvae. Histogram key: darkened = larvae on *Artemisia dracunculus*, cross-hatched = on *Artemisia arctica*, clear = on umbelliferous larval hostplants. Individuals are plotted on first component axis of PCA on combined character set and include only those used in original PCA. Regions refer to those indicated in Figure 10.

16


50%
N
nMB + SK
159
(17)
39
Duck Mt. to
Riding Mt. Pk.
90
(46)
8
(7)
sMB + nND
35
2
ON + WN
79
(74)
21
+1.6
-1.2
-3.2
Mo.
-2.4
0.0
+2.8
E4

17


N
s + cent. BC
67
Peace R.
46
central AB
49
sAB + SK
59
MB + ON
16
-1.0
+3.0
+6.5
Mo. + E4
■ A. dracunculus
▨ A. arctica
☐ Umbelliferae

✓

the result of interactions between *P. machaon* and *P. polyxenes*, rather than between *P. machaon* and *P. zelicaon* as in central Alberta. The dramatic effect of the gene for the black wing morph made it more difficult to demonstrate phenotypic intermediacy in morphometric characters and I was able to electrophorese only a small number of individuals from central Manitoba. However, populations scored on the second PC axis did tend to be intermediate in electrophoretic characters. Also a sizable proportion of black morph individuals in central Manitoba tend to take on character states found in *P. machaon*. For example, most have a club-shaped anal pupil and many have more yellow on the tegulae and apical forewing cell than in *P. p. asterius* from southern Ontario or the United States.

4.1.3 Adult characters versus larval foodplants

The separation of *P. machaon* from *P. zelicaon* and *P. polyxenes* on the basis of electrophoretic and morphometric characters was supported by a comparison between individuals collected as larvae on different foodplants. The scores of adults reared from *Artemisia* were plotted against those of individuals reared on various species of Umbelliferae, on the first PC axis derived from both the electrophoretic and the morphometric characters combined. This showed a fairly good separation between the foodplant groups in most regions (Figure 17). In the Peace River region the individuals reared on *Artemisia arctica* from alpine habitats grouped with those reared on *Artemisia dracunculus* from dry, grassy river banks. The *P. machaon* from southern Alberta and Saskatchewan, reared on *A. dracunculus*, were also separated from *P. zelicaon* on this basis, although their more similar morphometric characters result in a somewhat closer grouping. The single *P. machaon*-like individual reared from central Manitoba was obtained on umbellifers.

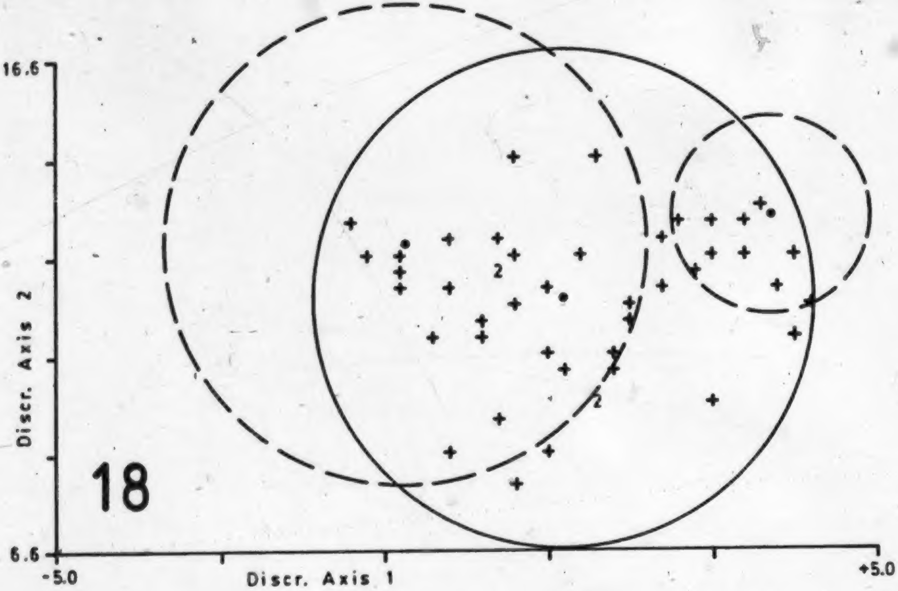
The specimens reared on *A. dracunculus* from central Alberta were collected at Nevis Junction, on a northward extension of prairie habitat along the Red Deer River. These adults resembled the *P. m. dodi* from further south along the river and were undoubtedly just an outlying population of this race. They also, however, resembled some specimens collected on umbellifers further to the west. Larvae of the hybrid populations from central Alberta feed on umbellifers, and in this respect are similar to *P. zelicaon*. Reared material showed the same wide range of phenotypes as the wild collected adults.

Since PCAs on the total sample from western Canada did not provide a very good separation between *P. machaon* and *P. zelicaon* from central and southern Alberta on the basis of morphometric characters, an attempt was made to do this by discriminant factor analysis (DFA) of foodplant groups. Three foodplant groups were defined. The first included all the specimens reared from *A. dracunculus* in either southern or central Alberta. The second included all the material from umbellifers in the southern Alberta region, all of

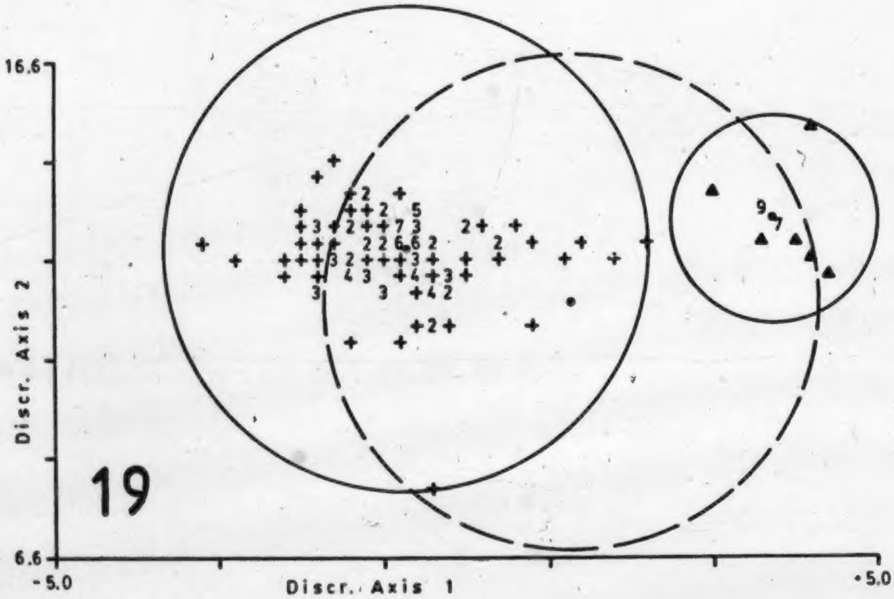
Figures 18 to 19. Reared adults plotted on discriminant axes, including only those used in original discriminant analyses. Numbers indicate more than one data point with the same coordinates. Circles indicate maximum diameters of the three original groups. Dashed lines indicate locations of populations from opposite figure.

Figure 18. 2D.DFA plot of reared samples: southern Alberta. On *A. dracunculus* (+) N=119; on umbellifers (triangles) N=22

Figure 19. 2D.DFA plot of reared samples: central Alberta. Only umbellifer-reared individuals shown, N=45



16.6
6.6
-5.0
+5.0
Discr. Axis 1
Discr. Axis 2
18



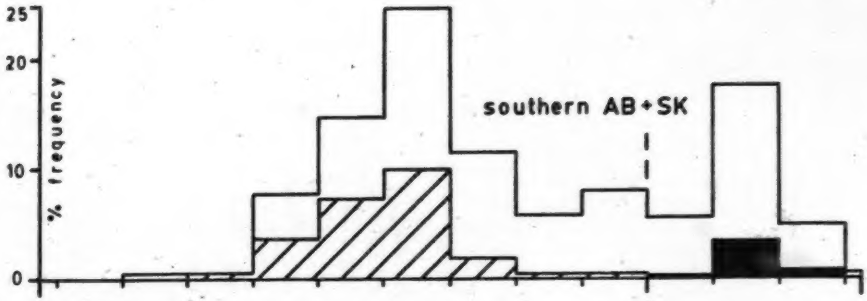
16.6
6.6
-5.0
+5.0
Discr. Axis 1
Discr. Axis 2
19

Figures 20 to 21. All adults from central and southern Alberta (AB), and southern Saskatchewan (SK), plotted on first discriminant axis. Reared individuals are indicated as subsets.

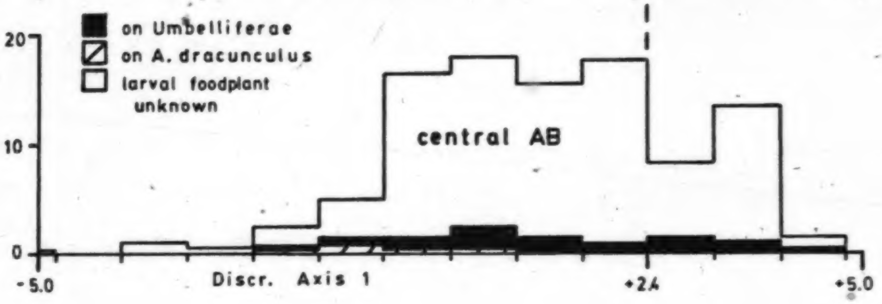
Figure 20. All southern AB and SK specimens, plotted on DFA.1. N=497, including N=119 reared from *A. dracunculus* and N=22 reared from umbellifers.

Figure 21. All central AB specimens, plotted on DFA.1. N=481, including N=7 reared from *A. dracunculus* and N=45 reared from umbellifers.

20


25
20
10
0
% frequency
southern AB + SK

21


■ on Umbelliferae
▨ on A. dracunculus
☐ larval foodplant unknown
20
10
0
central AB
-5.0
Discr. Axis 1
+2.4
+5.0

which were from *Angelica, Lomatium* or *Heracleum* in the Waterton Park and Crowsnest Pass area. The third group included all the adults reared from umbellifers in the central Alberta region. The morphometric characters used in this analysis were the same as those used in the PCAs, except that only 10 characters were used due to the fact that one character (tegula color) showed no variation in the groups defined above. The discriminant axis loadings are included in Table 17.

As with the PCAs on electrophoretic characters, the DFA gave a fairly good separation of *P. machaon* and *P. zelicaon* in southern Alberta (Figures 18-19). However, the umbellifer feeders from central Alberta did not separate very well from either of the other two groups. When all the wild collected adults from these regions were scored on the first discriminant axis (Figures 20-21), they showed a distribution of character combinations similar to that obtained from reared material. This indicated that the reared material probably included a representative sample of the foodplants which larvae of these populations feed on in nature.

4.1.4 Tests for Hardy-Weinberg equilibrium

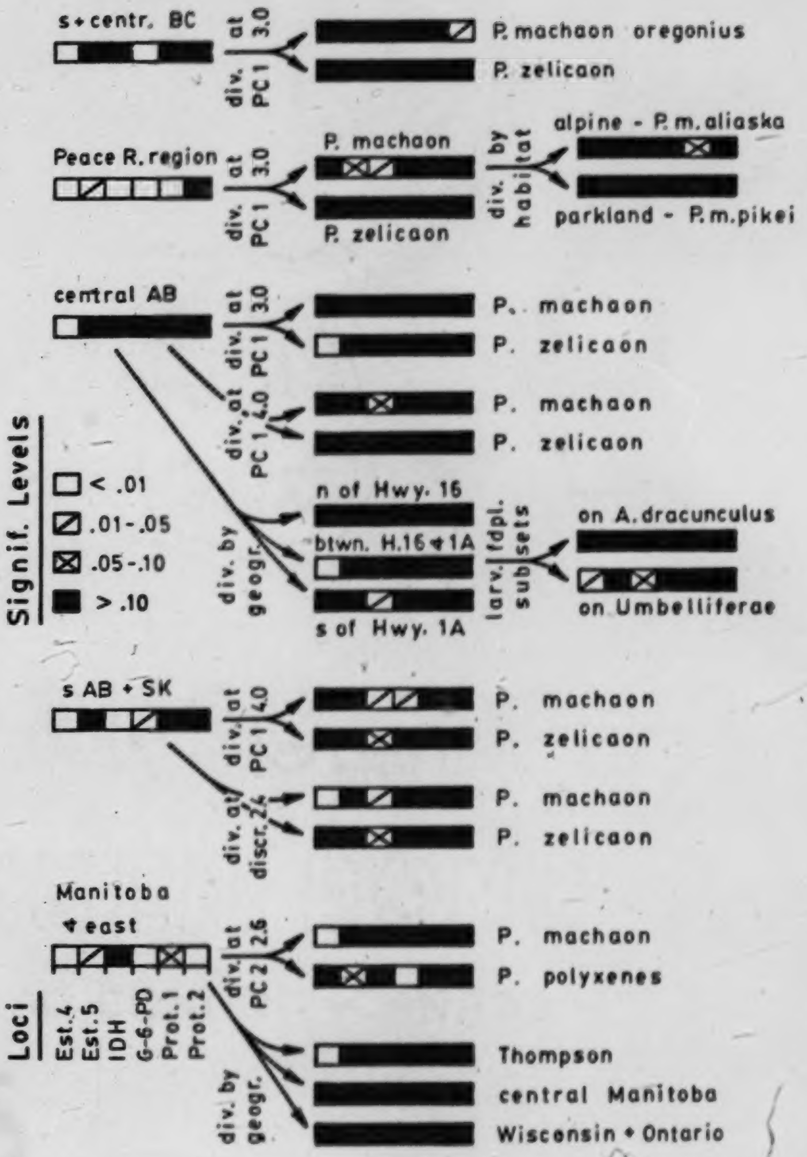
Chi-squared tests for deviation from Hardy-Weinberg (HW) proportions of enzyme genotypes can be used as an indication of whether or not gene flow occurs relatively freely within a population. A sample showing a significant excess of homozygous genotypes at a particular locus suggests some sort of genetic incompatibility between the different allelles. In the context of this study, I assume that homozygous excesses indicate the likelihood of assortative mating or higher heterozygote mortalities, which in turn suggest the presence of more than one species. I also assume that the different enzyme banding patterns are inherited, and for that reason I refer to "genes" rather than "electrophoretic characters" in this section.

Figure 22 includes all loci which showed a difference from HW proportions at the 10% level in at least one of the five major geographic regions. Six loci are included. Since numerous tests for HW equlibrium were performed, at least some of these are likely to show significant differences, due to sampling errors, when this really is not so for natural populations.

HW tests on the six loci showed that all five of the major regions had at least one locus with proportions of genotypes different from equilibrium at the 1% level. This suggested that more than one species might be present in each of the regions. However, the pattern of deviation from equilibrium, and the loci which deviated, were different in each of the regions.

In southern and central British Columbia, there were highly significant excesses of homozygous genotypes at the Est-4 and G-6-PD loci. These excesses disappeared when the total regional sample was divided into two groups on the

Figure 22. Hardy-Weinberg equilibrium tests on subpopulations. Six loci are shown as squares within bar for each population. Significance levels (key at center left) refer to deviation from equilibrium. Names for some populations refer to population divisions based on artificial criteria, such as arbitrary points on discriminant axes.


s + centr. BC
div. at PC 1 3.0
P. machaon oregonius
P. zelicaon
Peace R. region
P. machaon
P. zelicaon
div. by habitat
alpine - P. m. aliaska
parkland - P. m. pikei
central AB
P. machaon
P. zelicaon
div. at PC 1 4.0
P. machaon
P. zelicaon
div. by geogr.
n of Hwy. 16
btwn. H.16 + 1A
s of Hwy. 1A
larv. fdpl. subsets
on A. dracunculus
on Umbelliferae
Signif. Levels
☐ < .01
▨ .01-.05
☒ .05-.10
■ > .10
s AB + SK
div. at PC 1 4.0
P. machaon
P. zelicaon
div. at discr. 2.4
P. machaon
P. zelicaon
Manitoba + east
div. at PC 2 2.6
P. machaon
P. polyxenes
Loci
Est.4
Est.5
IDH
G-6-PD
Prot.1
Prot.2
div. by geogr.
Thompson
central Manitoba
Wisconsin + Ontario

22

basis of the clusters formed on the first PC axis of the analysis on both electrophoretic and morphometric characters, and the tests were rerun. This corroborates the hypothesis that there are two species in that region. The *P. m. oregonius* subsample showed an excess of heterozygotes of the Prot-2 locus which was significant at the 3.3 % level. No biological explanation is offered for this.

The total sample from the Peace River region showed large deviations from equilibrium in five of the six loci, all of which were due to homozygote excesses. When it was subdivided in the same way as for southern British Columbia, most of these excesses were eliminated in the *P. machaon* and *P. zelicaon* subsamples. A further subdivision of *P. machaon*, on the basis of the habitat the individual was collected in, eliminated the slight excesses in the Est-5 and IDH loci, and supported the division of *P. machaon* in this region into two ecological races, *P. m. aliaska* and *P. m. pikei*. However, a small homozygote excess showed up in *P. m. aliaska* in the Prot-1 locus. The biological significance of this, if any, is unknown, though a reasonably large allelle frequency difference at this locus between the two races should be noted.

The central Alberta regional sample was very different from the previous two, despite the fact that the total sample had fairly high frequencies of both of the pairs of alleles at the Est-4 and G-6-PD loci which normally distinguish *P. machaon* and *P. zelicaon*. The total sample contained genotypes which were not much different from equilibrium at any of the loci, except Est-5. When *P. machaon* was separated from *P. zelicaon* in the same way as for the Peace River and southern B.C. regions, the highly significant homozygote excess was retained in the *P. zelicaon* subsample. A division of the total sample at 4.0, rather than 3.0, on the same PCA axis showed a slightly significant excess of heterozygotes at the IDH locus. Clearly, the second division furnished subsamples more consistent with the hypothesis that there are two species in that region. However, it divided the total central Alberta sample down the middle of a somewhat bell-shaped curve of character combinations (Figure 12), and may simply reflect the large contribution of the Est-4 locus to the scores on that axis.

When the sample from the central Alberta region was divided into three subregions (a northern, middle and southern one), both the northern and southern subregions appeared not to be significantly different from equilibrium at the Est-4 locus either, despite the higher proportion of alleles characteristic of *P. zelicaon* in the northern subregion (ref. Table 8). This was especially interesting in the sample for the southern subregion, since it was composed of specimens from only a single locality at Bragg Creek. The deviation from equilibrium in the Bragg Creek sample at the IDH locus was caused by an excess of heterozygotes. The sample from the middle subregion continued to show an excess of homozygotes at Est-4. When the specimens reared on different foodplants were considered separately, it was clear that a slightly less significant excess remained at that locus. These adults were obtained from larvae collected on umbellifers, and all were on *Heracleum* plants.

The highly significant homozygote excess was retained even when the largest sample from a single locality in that subregion, Buck Lake, was considered separately (not shown on Fig. 22). This locality is, to the best of my knowledge, about 80 km from the nearest stand of *Artemisia dracunculus*. These results suggest that *P. machaon* and *P. zelicaon* have merged their gene pools in a large part of the central Alberta region, although not all loci are at equilibrium in the middle part of that region.

The regional sample from southern Alberta and Saskatchewan showed significant homozygote excesses at three loci. A division of the sample on the basis of scores on the first PCA axis of the analysis on both morphometric and electrophoretic characters eliminated the excess at the Est-4 locus, but only reduced it at the IDH and G-6-PD loci. When the sample was divided on the basis of scores on the first axis of the discriminant analysis of reared specimens, the homozygote excesses were retained at the Est-4 and IDH loci. The division of the sample from this region into two species is supported by the fact that the homozygote excesses were partially reduced even when the sample was subdivided on the basis of just morphometric characters.

However, this subdivision is far from being as good as that effected in the southern British Coumbia and Peace River regions. One reason may be a higher probability of incorrect species assignment, due to the greater morphometric similarity between *P. machaon* and *P. zelicaon* from this region.

A second explanation is that, even though the species retain a separate genetic identity, there is a biologically significant amount of gene introgression between the species. The rate of introgression may differ between loci, as for example between Est-4 and G-6-PD. This suggestion is supported by the fact that these two loci have very similar allele frequency differences between *P. machaon* and *P. zelicaon* in the southern British Columbia and Peace River regions, and yet G-6-PD seems to have reached equilibruim before Est-4 in the middle part of the hybrid zone in central Alberta.

In the region which included samples from Manitoba, Wisconsin and Ontario, there was also evidence for two species, with some hybridization between them. Here the main allelles distinguishing between *P. polyxenes* and *P. machaon* were G-6-PD and Prot-2, rather than G-6-PD and Est-4, as between *P. zelicaon* and *P. machaon*. The total regional sample had several significant deviations from equilibrium. When it was divided on the basis of scores on the second PCA axis of the run on both morphometric and electrophoretic characters, which essentially separated black morph from yellow morph individuals, then a highly significant deviation remained at the G-6-PD locus in the sample comprised of black morph specimens. These deviations were eliminated when the region was divided geographically into three subregions. The main difference from the previous subdivision was that one yellow morph and nine black morph specimens were placed in a group by themselves. Under both schemes there was a significant excess of homozygotes in the Est-4 locus of the northern Manitoba sample. This was due to the presence at Thompson of 2 individuals homozygous for the "B" allele (most common in *P. zelicaon*), compared with only 4 heterozygous individuals and 33 individuals homozygous for the "A" allele (most common in *P. machaon* and *P. polyxenes*). I can offer no convincing biological explanation for this situation, since Thompson is many hundreds of km from the nearest localities where *P. zelicaon* specimens have been found. Instead I suspect it may be due to sampling error. Clearly there is more work needed to ascertain species relationships in Manitoba.

4.2 Diagnosis of Adults and Ranking of Taxa

For the purpose of quantitatively tabulating character variation, 13 major populations were defined. The arrangement of these groups was based on both electrophoretic and morphometric characters, and the groups resemble those described in the previous sections involving multivariate analyses and Hardy-Weinberg equilibria. The table about electrophoretic characters (Table 7) includes some specimens for which not all loci were scored, but for which it was possible to be certain of their identification by reference to their morphometric characters. The table for morphometric characters (Table 6) includes data for only those specimens used in the PCAs.

4.2.1 *Papilio machaon*

In general, *P. machaon* adults from western Canada were distinguished by yellow hair on the ventral part of the thorax and abdomen, yellow scales covering most of the forewing disc on the ventral side, and the anal pupil connected to the wing margin, whether club shaped or a thin line. This result verifies the utility of the adult color pattern characters used by others to identify this species. In electrophoretic characters, *P. machaon* individuals were distinguished by the A allele at Est-4, the C allele at G-6-PD and a relatively high proportion of D alleles at IDH.

P. m. dodi specimens were more difficult to identify in the absence of electrophoretic information, but could best be distinguished from the *P. zelicaon* populations sympatric with them by the club shaped, connected anal pupil. I have examined the types of *P. m. dodi* in the Canadian National Collection, and they definitely belong to the race of *P. machaon* whose larvae feed on *Artemisia dracunculus* on the prairies of southern Alberta and Saskatchewan.

Table 6. Morphometric character state distributions

Abbreviations: n of H.16 = central Alberta region, north of Highway 16, Hwy. 16-1A = central Alberta region between Highways 16 and 1A, s+c BC = southern and central British Columbia, s AB = southern Alberta.

		Papilio machaon					*Papilio zelicaon* X *machaon*			*Papilio zelicaon*			*Papilio polyxenes*	*Papilio polyxenes*
Character	State	*oregonius*	*aliaska*	*pikei*	*hudsonianus*	*dodi*	n of H.16	Hwy. 16-1A	Bragg Cr.	s+c BC	Peace area	s AB	*asterias*	X *machaon*
	N:	55	41	79	37	147	62	90	72	12	50	52	21	10
1. DHW anal yellow	1	5.5	92.7	49.4	94.6	23.1	72.6	72.2	72.2	75.0	74.0	84.6	100.0	90.0
	2	27.3	7.3	34.2	5.4	51.7	24.2	24.4	23.6	16.7	22.0	11.5		10.0
	3	56.4		16.6		25.2	3.2	3.3	4.2	8.3	4.0	3.8		
	4	10.9												
2. DHW pupil shape	1	7.3	87.8	43.0	10.8	2.7	3.2	1.1						
	2	83.6	12.2	51.9	86.6	81.0	14.5	41.1	68.1	8.3	2.0		4.8	80.0
	3	9.1		5.1	2.7	14.3	32.3	31.1	27.8		20.0	5.8	61.9	20.0
	4					2.0	50.0	26.7	4.2	91.7	78.0	94.2	33.3	
3. DHW blue/red sep.	1	36.4	82.9	77.2	32.4	2.7	8.1	7.8	5.6					10.0
	2	32.7	17.1	19.0	29.7	17.7	11.3	25.6	29.2		8.0	1.9		20.0
	3	30.9		3.8	37.8	79.6	80.6	66.7	65.3	100.0	92.0	98.1	100.0	70.0
4. tegula color	1	100.0	100.0	100.0	100.0	99.3	100.0	98.9	98.6	100.0	100.0	100.0		30.0
	2					0.7		1.1	1.4				19.0	40.0
	3												81.0	30.0
5. VFW discal color	1	100.0	92.7	100.0	89.2	10.2	11.3	4.4	11.1		2.0			
	2		7.3		8.1	22.4	16.1	15.6	11.1		10.0			
	3					29.3	24.2	33.3	19.4	16.7	28.0	5.8		10.0
	4				2.7	38.1	48.4	46.7	58.3	83.3	60.0	94.2	100.0	90.0
6. VFW apical smudge	1	100.0	100.0	100.0	100.0	100.0	100.0	96.7	93.1	100.0	100.0	96.2		20.0
	2							3.3	6.9			3.8	33.3	30.0
	3												66.7	50.0

Table 8. continued

Character	State	*Papilio machaon*					*Papilio zelicaon* X *machaon*			*Papilio zelicaon*			*Papilio polyxenes asterias*	*Papilio polyxenes* X *machaon*
		oregonius	*aliaska*	*pikei*	*hudsonianus*	*dodi*	n of H.16	Hwy. 16-1A	Bragg Cr.	s+c BC	Peace area	s AB		
7. VHW postmed. orange	1-2	12.8	34.1	70.9	45.9	5.4	8.0	7.7	4.2	8.3	8.0	1.9		
	3-4	80.0	65.9	29.1	54.1	88.2	80.6	77.8	72.2	91.7	82.0	80.4		10.0
	5-6	7.2				2.0	9.7	3.3	11.1		8.0	7.7		20.0
	7-8					4.0	1.6	11.2	12.5		2.0		100.0	70.0
8. metathoracic color	1	100.0	100.0	100.0	100.0	27.2	11.3	12.2	20.8		4.0			10.0
	2					71.4	88.7	76.7	58.3	100.0	96.0	82.7		
	3					1.4		11.1	20.8			17.3	100.0	90.0
9. abd. ventral line	1-3	98.2	100.0	100.0	100.0	21.8	12.9	10.0	16.7		4.0			
	4-5	1.8				6.1	87.1	4.4	4.2					10.0
	6-7					9.5		2.2	5.6			1.9		
	8-9					62.2		81.1	73.6	100.0	96.0	98.1	100.0	90.0
10. abd. lateral line	1	100.0	100.0	100.0	100.0	98.6	100.0	93.3	90.3	100.0	100.0	90.4		10.0
	2					1.4		1.1	1.4			1.9		
	3							5.6	8.3			7.7	100.0	90.0
11. abd. upper line	1-3								4.2					90.0
	4-5				16.2			6.7	9.7			1.9		
	6-7		14.7	2.5	45.9	3.4	3.2	13.3	23.6			3.8		
	8-9	100.0	85.3	97.5	37.8	96.6	96.8	80.0	62.5	100.0	100.0	94.2	100.0	10.0

Table 7. Allele frequencies, by region and taxon

Abbreviations: see caption for Table 6.

Locus	Allele	*Papilio machaon*					*Papilio machaon X zelicaon*			*Papilio zelicaon*			*Papilio polyxenes asterias*	*Papilio polyxenes X machaon*
		oregonius	*aliaska*	*pikei*	*hudsonianus* (Thompson)	*dodi*	n of Hwy 16	Hwy 16 to 1A	Bragg Creek	cent. + s BC	Peace region	s AB	WN + ON	cent. MB
aGPD	(n)	57	50	92	39	170	76	102	79	12	61	60	21	10
	A											0.017		
	B	0.974	1.000	1.000	1.000	1.000	0.993	1.000	0.994	1.000	1.000	0.975	1.000	1.000
	C	0.026					0.007		0.006			0.008		
G-6-PD	(n)	55	50	90	39	157	66	96	74	12	61	56	21	10
	E										0.008			
	A		0.020	0.128	0.038	0.006	0.136	0.047	0.027		0.016			0.200
	B	0.073	0.010	0.039	0.026	0.089	0.455	0.370	0.385	0.958	0.762	0.759		0.050
	I	0.064		0.011		0.092								0.050
	K			0.006		0.003	0.030	0.026	0.007		0.016	0.008	0.976	
	C	0.800	0.970	0.817	0.936	0.739	0.311	0.510	0.554	0.042	0.172	0.214	0.024	0.700
	D	0.064				0.070	0.038	0.042	0.027		0.025	0.018		
IDH	(n)	55	50	85	39	154	63	96	74	12	61	56	21	10
	A	0.091			0.026	0.045	0.008	0.057	0.007					
	B	0.664	0.720	0.947	0.679	0.545	0.873	0.724	0.689	1.000	0.984	0.938	1.000	0.900
	C	0.045	0.020		0.026	0.049	0.008	0.026	0.027			0.036		
	D	0.182	0.260	0.053	0.269	0.360	0.111	0.193	0.277		0.016	0.027		0.100
	E	0.018												
MDH	(n)	57	50	93	39	165	70	102	74	12	63	17	21	10
	I									0.042		0.018		
	A		0.030	0.005	0.038	0.006	0.021	0.054	0.047			0.009		
	B	1.000	0.970	0.995	0.962	0.988	0.979	0.946	0.946	0.958	1.000	0.964	0.976	0.950
	C					0.006			0.007			0.009	0.024	0.050
ME	(n)	55	50	91	39	162	71	96	79	12	61	56	21	10
	J	0.009											0.071	
	I	0.164	0.010		0.077	0.046	0.021	0.010	0.038	0.083			0.071	0.100
	A	0.291	0.170	0.242	0.244	0.185	0.056	0.047	0.051	0.125	0.074	0.027	0.143	0.100
	B	0.536	0.820	0.758	0.641	0.707	0.908	0.901	0.880	0.792	0.893	0.857	0.643	0.750
	K					0.006	0.014	0.010				0.027		0.050
	C				0.038	0.052		0.031	0.032		0.033	0.089	0.048	
	D					0.003							0.024	

Table 7. continued

Locus	Allele	*Papilio machaon*					*Papilio machaon X zelicaon*			*Papilio zelicaon*			*Papilio polyxenes asterias*	*Papilio polyxenes X machaon*
		oregonius	*aliaska*	*pikei*	*hudsonianus* (Thompson)	*dodi*	n of Hwy 16	Hwy 16 to 1A	Bragg Creek	cent. + s BC	Peace region	s AB	WN + ON	cent. MB
ODH	(n)	55	48	84	39	156	63	96	74	12	59	56	21	10
	A	0.009	0.021		0.115	0.006	0.040	0.063	0.162		0.102	0.036		0.050
	B	0.991	0.760	0.958	0.795	0.994	0.857	0.875	0.811	1.000	0.822	0.946	1.000	0.950
	C		0.219	0.042	0.090		0.103	0.063	0.027		0.076	0.018		
APK	(n)	55	45	82	39	154	63	96	74	12	53	56	21	10
	A											0.009		
	B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.991	1.000	1.000
EST-4	(n)	59	50	98	39	163	75	102	79	12	61	59	21	10
	A	1.000	0.920	0.954	0.897	0.954	0.293	0.475	0.677		0.074	0.085	1.000	0.950
	B		0.080	0.046	0.103	0.046	0.707	0.525	0.323	1.000	0.925	0.915		0.050
EST-5	(n)	59	50	96	39	163	75	102	79	12	61	56	21	10
	I	0.008				0.009			0.006					
	A	0.297	0.080	0.510	0.077	0.337	0.053	0.108	0.146		0.049	0.071		0.150
	B			0.010	0.013		0.007				0.008			0.050
	C	0.695	0.920	0.479	0.910	0.653	0.893	0.873	0.842	0.958	0.902	0.929	0.952	0.800
	D						0.047	0.020	0.006	0.042	0.041		0.048	
Prot-1	(n)	55	45	82	39	154	63	96	74	12	52	56	10	21
	A	1.000	0.789	0.598	0.897	0.997	0.976	0.969	0.926	1.000	0.952	1.000	1.000	1.000
	B		0.211	0.402	0.103	0.003	0.278	0.060	0.375		0.048			
Prot-2	(n)	55	45	82	39	154	63	96	74	12	52	56	10	21
	I				0.064	0.026		0.010	0.007		0.019			
	A	0.400	0.022	0.018	0.038	0.224	0.071	0.130	0.088	0.333	0.135	0.455	0.976	0.500
	B	0.600	0.956	0.970	0.897	0.727	0.921	0.844	0.905	0.667	0.837	0.536	0.024	0.500
	C		0.022	0.012		0.023	0.008	0.016			0.010	0.009		
Heterozygosity:		0.233	0.155	0.188	0.203	0.218	0.196	0.219	0.246	0.076	0.162	0.158	0.191	0.078

Subspecies of *P. machaon* in western Canada were best separated from each other by locality and habitat, though there were major changes in the frequency of particular states of several characters, including IDH, ODH, Est-4, Prot-1 and Prot-2. Though almost all specimens of *P. m. oregonius* and *P. m. dodi* from western Canada can be distinguished by both adult and larval color pattern, these two subspecies grade into each other in western Montana and southern Idaho. Since the zone of intergradation is narrow, relative to the phenetically more homogeneous ranges of the subspecies, I recognize the populations on either side of the continental divide in Montana and northward as separate subspecies.

I am uncertain of the extent and location of the intergradation between these subspecies south of Montana. In Utah and Colorado, the black adult wing morph becomes more common (Emmel, 1975) and the name *P. machaon bairdii* should be applied. The name *P. brucei* has been applied to yellow morph adults in polymorphic populations within the range of *P. m. bairdii*. Its type locality is from the northern part of the major clinal shift to yellow forms, and its use in a subspecific sense is probably not of much value. I follow the practice of Fisher (1980) and Miller and Brown (1981) in treating the name as a junior synomym of *P. m. bairdii*.

The previous subdivision of the southern subspecies of *P. machaon* as separate species is probably a consequence of

W.H. Edwards' relatively typological species concept, and the natural tendency of many workers to view the black morph adults as fundamentally different from the yellow morph adults. However, black morph adults of *P. machaon* occur in low frequencies as far north as Drumheller, Alberta, where they are electrophoretically identical to the yellow morph adults. Hence, I feel that the inclusion of *P. bairdii* in *P. machaon* is an inescapable consequence of the application of the biological species concept to geographic clines.

4.2.2 *Papilio zelicaon* and hybrids

P. zelicaon individuals from western Canada could generally be recognized by the black hair on the ventral part of the thorax and abdomen, black or almost black ventral forewing disc and the rounded, centered anal pupil. As in *P. machaon*, these characters match those previously used in traditional taxonomic treatments. Important diagnostic electrophoretic characters included the B allele in both the Est-4 and G-6-PD loci.

I do not believe that any formal subspecific divisions should be recognized in *P. zelicaon*. The species is composed of innumerable slightly differentiated populations, all of whose adult features appear to grade into each other. Local foodplant and climatic adaptations of most populations are usually far more pronounced than are the relatively minor differences in morphometric characteristics. I believe that the recent practice, of referring to the populations which

Remington (1968a) named *P. gothica* as *P. zelicaon nitra*, is unwarranted. Yellow morph adults are more common than the black form even at the type locality of *P. nitra*, and I find the eastern and western yellow morphs of *P. zelicaon* to be impossible to separate with any degree of consistency.

The presumed type of *P. zelicaon* Lucas was examined for me in considerable detail by G.E. Ball in 1980, on a trip he made to the Paris Museum. Using Ball's description and comparative material, as well as photographs which were taken of the specimen, features of the type of *P. zelicaon* were checked against Remington's (1968a) diagnosis of *P. gothica*. The specimen is closer to Remington's conception of *P. gothica* than his conception of *P. zelicaon*. This is not surprising, since as Shapiro (1975) and Emmel and Shields (1980) pointed out, *P. zelicaon* from the type locality in central California has undergone basic ecological changes since its description in 1852, while the remaining populations at higher altitudes in central California are still very similar in appearance to topotypic *P. gothica*.

In some regions, particularly central Alberta, there was a high proportion of individuals with intermediate character states, or character combinations which placed them in an intermediate position between *P. zelicaon* and *P. machaon*. These were considered to be hybrids, and such individuals formed the majority of some populations. Since these populations included individuals with phenotypes occupying the complete range between the typical parental forms, many individuals were difficult to identify as hybrids. Hybrid populations were also highly variable in composition, and were only identified as such when they showed a a unimodal distribution of phenotypes, of which the peak was clearly intermediate between the parental species.

The *P. zelicaon X machaon* hybrid swarms in the Cypress Hills have been much less completely documented than those in central Alberta. I designate these populations as hybrid swarms mainly because most individuals look very similar to the hybrid material collected in the southern part of central Alberta. As well, they are intermediate in wing and body pattern between the *P. machaon* and *P. zelicaon* specimens collected in the prairie habitats surrounding the Cypress Hills.

In regions where hybridization between *P. zelicaon* and *P. machaon* is rare, it is possible that there are structural isolating mechanisms between the species, in addition to behavioral ones. This was suggested by the only natural interspecific mating which I have observed in such regions of sympatry. The mating took place at Taylor, at a site where *P. m. pikei* adults are common, and involved a fresh *P. zelicaon* female and slightly worn *P. machaon* male. They remained in copula for at least 11 hours before they separated. Such an abnormally long mating (Clarke and Sheppard, 1956b) may be an effect due to the the disturbance of being netted, but seems more likely to be due to some sort of prezygotic mating disfunction.

4.2.3 *Papilio polyxenes* and hybrids

Most specimens of *P. polyxenes* were easily distinguished from those of *P. zelicaon*, *P. machaon* and their hybrids by the much greater amount of black scales on the hindwing, covering more than half of the hindwing disc, and yellow spots rather than a broad yellow band on the sides of the abdomen. Separation was also based on the K allele of G-6-PD and the A allele of Prot-2.

A small proportion of *P. polyxenes*-like individuals were noted in *P. zelicaon*, *P. machaon* and their hybrids in western Canada. These, however, had the same electrophoretic alleles as the yellow morph individuals they were found with, and could also be distinguished from *P. polyxenes* by the greater amount of yellow on the tegula and apex of the forewing, as well as the lesser amount of orange on the postmedian band of the ventral hindwing. Since the black morph specimens of *P. zelicaon* from Alberta prairies were identical in appearance to a series which I have seen from the type locality of *P. nitra* in the Judith Mountains, there is no reason to expect these individuals to comprise a separate species in Montana, either. Although the morphometric differences between *P. zelicaon* and *P. polyxenes* in western Canada suggest a greater ease of species identification than Fisher (1980) reported in Colorado, I expect that I would have found similar difficulties if I had been able to obtain a larger sample from localities where these two species are in closer contact in southern Saskatchewan.

Since the interactions of *P. polyxenes* with *P. machaon* and *P. zelicaon* in western Canada are not well understood, I rely on the opinions of authors who are familiar with the three species in the western United States (eg. Ferris and Emmel, 1982; Fisher, 1977 and 1980). These authors have consistently reported that *P. polyxenes* maintains a distinct genetic identity from both *P. zelicaon* and *P. machaon* throughout most of their region of potential interaction. As well, although electrophoretic characters indicate some intermediacy in central Manitoba, it should be noted that samples of *P. polyxenes* from Ontario and Wisconsin are as different from *P. zelicaon* and *P. machaon* as these two species are from each other.

Most of the specimens of *P. polyxenes* from southern Manitoba are indistinguishable in appearance from *P. p. asterius* from Ontario and the eastern United States. The remainder show signs of introgression with *P. machaon*. Specimens exhibiting substantial introgression are designated as *P. polyxenes X machaon* hybrids. The identification of such natural hybrid specimens is supported by comparisons with those obtained by artificial hybridization. In particular, many of the adults collected in central Manitoba appear very similar or identical to the hybrids obtained by other workers (see particularly Clarke and Sheppard, 1953, 1955a; Ae, 1961, 1964; Remington, 1958, 1968a). The same applies to hybrid specimens of *P. zelicaon* and *P. machaon* from central Alberta. These studies clearly indicate the genetic basis of these characters, and for this reason I have used several of these characters in the morphometric portion of this study. I consider the similarity between the experimentally produced and wild-collected specimens to be strong evidence for the hybrid origin of the collected material.

Two taxonomic descriptions refer to adult forms which are due to hybridization between *P. polyxenes* and *P. machaon*. These are *P. kahli* and *P. m. avinoffi*, both of which are referred to in this study either as black or yellow wing morph adults of *P. polyxenes X machaon*, or as *P. polyxenes X machaon* and *P. machaon X polyxenes*, respectively. My use of these names is based on photographs I have seen of the holotypes. I have also seen several paratypes, but these differ slightly from one another, as well as from the holotype. At least one of the female paratypes of *P. kahli* in the Canadian National Collection seems to me to be identical to typical *P. p. asterius* specimens. My opinion was apparently shared by J.D. McDunnough, who indicated his opinion on a folded slip of paper attached to the specimen pin.

Specimens which fit the description of *P. m. avinoffi* were obtained by Remington (1958, 1968a), when he crossed two comparatively yellowish black adult morph individuals from central Manitoba, and got some yellow morph as well as black morph offspring. The *avinoffi* form tends to grade into more typical *P. m. hudsonianus* and so identification of specimens is arbitrary.

The systematic relationship of *P. polyxenes* and *P. machaon* in central Manitoba clearly needs more investigation than I have provided in the present study. The recognition of central Manitoba populations as interspecific hybrid populations, rather than as intermediates between subspecies, allows the retention of established taxonomic practice, pending a more thorough study of these two taxa in this region, as well as elsewhere in their ranges.

4.2.4 Ranking and accuracy of identification

The distribution of morphometric and electrophoretic character states showed, in several ways, that more than one species of the *P. machaon* group was present in western Canada. First, multivariate analysis of either of these two character suites indicated three major clusters of individuals in western Canada, and two major clusters in each of four of the five regions in western Canada. Second, enzyme allele genotypes suggested interruptions to gene flow which corresponded to the breaks between clusters in most of western Canada. Third, the morphometric and electrophoretic character distributions showed good correspondence with each other, as well as with ecological features such as preferred habitat and larval foodplant. This character concordance applied to areas where there appeared to be a large amount of interspecific hybridization, as well as those in which species appeared to interbreed very little. The characters of wing and body color pattern, which had been used by taxonomists in the past to distinguish between species, largely held up under critical examination. A few electrophoretic loci were also diagnostic for species, and so gave additional information about inter and intrapopulation relationships.

However, since there was evidence of hybridization between each of the three species, the ranking of some populations as species, and others as interspecific hybrid swarms or subspecies, was partially arbitrary. This was resolved by an arrangement that reflected the fact that species hybridize only rarely over most of their sympatric range, and which also involved a minimum of change in existing taxonomic arrangements. Since previous taxonomic arrangements were not based on electrophoretic characters, consideration of this character suite allowed an independent confirmation of the biological significance of these arrangements.

The electrophoretic characters also allowed a more direct comparison with the degree of genetic similarity between species of other, unrelated, taxa. This comparison was obtained by calculating Nei's (1972) Genetic Identity (*I*) for all combinations of each of the 13 geographically separated populations of the *P. machaon* group which showed little or no internal interruption in gene flow. Nei's Genetic Identity is the most commonly used of several standardized genetic similarity coefficients, and *I* has been determined for a wide variety of taxa.

Of the 13 major populations distinguished in this study, all pairs listed as separate species had *I* values less than or close to 0.85 (Table 8). These pairs included those populations from the three regions in which *P. machaon* and *P. zelicaon* occur sympatrically. Thorpe (1982) showed that when two populations have an *I* value of less than 0.85, the probability is very high that they are distinct species. Thus, despite difficulties in separating individuals of some populations on the basis of morphometric characters, as well as the presence of several hybrid swarms, genetic similarity coefficients based on elctrophoretic characters suggest that at least the main clusters were different enough to rank as separate species.

I values can also be used to make intraspecific pairwise comparisons. About 80% of conspecific I values are above 0.95 (Thorpe, 1982). In the present study, all the comparisons of populations within *P. machaon* and *P. zelicaon* were close to or above 0.95.

The interval between 0.85 and 0.95 is occupied by a few values from interspecific pairs and a much larger proportion of intraspecific pairs. In the *P. machaon* group, those comparisons which involve hybrid swarms and one of the parental species generally show *I* values between 0.85 and 0.95. Several of these, however, resemble one parental species more than the other and show *I* values above 0.95

Table 8. Nei (1972) Genetic Identity and Distance.

Mean genetic identity is below diagonal and mean genetic distance is above diagonal.

Population	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. *P.m. oregonius*	*****	0.043	0.053	0.029	0.010	0.124	0.072	0.054	0.226	0.196	0.179	0.017	0.145
2. *P.m. aliaska*	0.958	*****	0.038	0.006	0.032	0.094	0.052	0.032	0.234	0.170	0.192	0.047	0.233
3. *P.m. pikei*	0.948	0.963	*****	0.045	0.046	0.123	0.086	0.063	0.258	0.195	0.219	0.062	0.249
4. *P.m. hudsonianus*	0.972	0.994	0.956	*****	0.022	0.191	0.049	0.029	0.221	0.165	0.181	0.038	0.217
5. *P.m. dodi*	0.990	0.969	0.955	0.978	*****	0.102	0.053	0.034	0.217	0.176	0.172	0.027	0.177
6. *P.m.X z.*:n of H.16	0.884	0.911	0.884	0.913	0.903	*****	0.010	0.028	0.039	0.014	0.031	0.097	0.232
7. *P.m.X z.*:Hwy 1A-16	0.930	0.949	0.918	0.953	0.949	0.990	*****	0.007	0.069	0.039	0.048	0.058	0.202
8. *P.m.X z.*:Bragg Cr.	0.947	0.968	0.939	0.971	0.967	0.972	0.993	*****	0.108	0.069	0.083	0.048	0.204
9. *P.zelicaon* : s. BC	0.797	0.791	0.773	0.802	0.805	0.962	0.933	0.898	*****	0.011	0.008	0.188	0.267
10. *P.zelicaon* : Peace	0.822	0.843	0.823	0.848	0.838	0.986	0.961	0.933	0.989	*****	0.013	0.161	0.276
11. *P.zelicaon* : s. AB	0.836	0.826	0.803	0.835	0.842	0.970	0.953	0.920	0.992	0.987	*****	0.140	0.219
12. *P.m. X p.*: c. MB	0.984	0.954	0.940	0.962	0.974	0.908	0.943	0.953	0.829	0.851	0.870	*****	0.109
13. *P.polyxenes*	0.865	0.792	0.780	0.805	0.838	0.793	0.817	0.815	0.766	0.758	0.803	0.897	*****

when compared with the more similar species. For example, the northern part of the *P. machaon X zelicaon* swarm is closer to *P. zelicaon*, while the southern part (Bragg Creek) is more similar to *P. machaon*. This result could have been expected on the basis of morphometric character similarities. However, the central Manitoba population is much more like *P. machaon* than *P. polyxenes*, a result in contrast to that which might be expected on the basis of morphometric similarities (for rough comparisons see 3D PCA scores in Figures 7-9).

Without information about locality, habitat or electrophoretic alleles, I estimate that I am able to correctly identify 95% of all specimens from western Canada as members of one of the groups listed in the key in the previous chapter. My accuracy is probably higher for distinguishing *P. machaon* from *P. zelicaon* in the absence of a large hybrid swarm. *P. zelicaon X machaon* and *P. polyxenes X machaon* hybrids, as well as *P. m. dodi*, are more difficult to distinguish from each other and I estimate that I can correctly identify about three quarters of all such specimens with only morphometric information.

Diagnosis of specimens on the basis of morphometric characters in the key was found to be fairly reliable when compared to scores obtained from PCA factor loadings. Several characters used in the keys were not used in the original multivariate character analyses, generally because they were difficult to score consistently. Both the key and PCA factors produce arbitrary divisions which are not particularly meaningful in hybrid populations.

Since the five subspecies of *P. machaon* are allopatric, or parapatric and separated by habitat in western Canada (see next chapter), it is possible to obtain a more precise estimate of accuracy of identification. Using habitat and geographic range to define groups, I performed a discriminant function analysis on the five subspecies, using the morphometric and electrophoretic characters which were employed in the multivariate analyses in previous sections. Since sample sizes were small, only the 27 variables which showed more than 10% variation in frequency between groups were used. The results are contained in Table 9.

This analysis indicates that a high frequency of correct identification can be achieved for these taxa if both major character suites are used. The lowest accuracy, 76% for *P. m. hudsonianus*, is still fairly high. If only the 11 morphometric characters listed in Table 2 are used in a new DFA, rather than the 27 morphometric and electrophoretic characters used to obtain the results in Table 9, then the lowest accuracy is 62%, again for *P. m. hudsonianus*. However, if forewing length and tail length are added to these 11 characters, and a third DFA is performed, then the accuracy of correct identification of *P. m. hudsonianus* rises to 70%, and the lowest is 68%, for *P. m. pikei*. I estimate that my personal lowest accuracy of identification

Table 9. Frequency of correct identification of subspecies of *Papilio machaon*.

Values based on discriminant function analysis (DFA) of 27 morphometric and electrophoretic characters. Classification percent shows frequency of correct identification (eg. 82.9% for *P. m. aliaska*) and incorrect identification (eg. 9.8 and 7.2 % of *P. m. aliaska* were misclassified as *P. m. hudsonianus* and *P. m. pikei*, respectively).

		% Classification with DFA				
Defined Groups	**N**	**1.**	**2.**	**3.**	**4.**	**5.**
1. *P. m. aliaska*	41	82.9	9.8	7.3		
2. *P. m. hudsonianus*	37	16.2	75.7	8.1		
3. *P. m. pikei*	79	7.6	1.3	88.6	2.5	
4. *P. m. oregonius*	55	1.8		1.8	96.4	
5. *P. m. dodi*	147			1.4	7.5	91.2

of these five *P. machaon* subspecies is 75% if characters such as wing shape and color are considered, which are difficult to quantify for computer work.

It is difficult to obtain a precise assessment of the relative systematic utility of morphometric and electrophoretic characters in the context of the present study. The morphometric characters were chosen on the basis of their variability within western Canada, and also as a means of comparison to systematic descriptions and diagnoses. Electrophoretic characters were selected much more randomly, since any protein that showed consistent, simple banding patterns was used. As well, only three loci showed more than 50% allele frequency differences between populations, and there was a reasonable possibility that results would be affected by sampling error. Furthermore, the coding scheme for morphometric characters was somewhat different from that used for electrophoretic characters in the principal components analyses. A more strictly analogous scheme would have reduced the number of electrophoretic characters from 42 to 10, a number more comparable to the 11 morphometric characters used. Despite these factors, it is clear that electrophoretic analysis is of considerable systematic utility (*cf* Wake, 1981). The large degree of correspondence of the two types of characters in the context of the present study is a demonstration of the potential usefulness of electrophoretic analysis in systematic research on species complexes.

4.3 Larval Color Pattern

4.3.1 General pattern

Larvae of *P. machaon*, *P. zelicaon* and *P. polyxenes* do not show consistent interspecific differences in color pattern, though there is a fair degree of intraspecific variability. The larvae of *P. alexanor* have a color pattern which is very similar to that of the above three species, despite a very different adult wing pattern. *P. indra* and *P. hospiton* each have a larval color pattern which is divergent from that of the other species in the *P. machaon* group, but which is more similar to that of other *P. machaon* group members than to other *Papilio*.

Larval color pattern is relatively uniform in the first three instars, while the pattern on fourth and fifth instar larvae is much more variable. The color pattern of fourth instar larvae varies from a banded pattern very similar to that of fifth instar larvae, to a pattern more like that of the first three instars, where the larva is predominantly black with a white dorsal patch and very small colored spots at the bases of the tubercles. I have found the more darkly patterned fourths most frequently in hybrid populations in the Alberta foothills, as well as in *P. m. aliaska* from Pink Mountain, British Columbia. Tubercle size of larvae varies as well, with *P. m. aliaska* fourth instar larvae generally having the smallest tubercles and *P. zelicaon* larvae having the largest. These tubercles are absent from fifth instar larvae.

Most fifth instar *P. machaon* group larvae are predominantly green, with a prominent black band extending around each segment, and six colored spots on most segments. Within populations, the background green color varies from pale bluish-green to bright emerald green, and the black bands vary considerably in width. In *P. indra*, the black bands are especially broad, and in some larvae the ground color is pink or white, rather than green (Emmel, 1975). In *P. hospiton* and some North African subspecies of *P. machaon*, the black segmental bands are longitudinally oriented reticulations. The color of the segmental spots varies from lemon yellow to orange-red within the *P. machaon* group, and will be dealt with in detail below.

Variation in the extent of the dark markings of the fourth and fifth instar larvae may be affected by environmental conditions. Tyler (1975, p.51) reports that some *P. zelicaon* larvae reared under a cool temperature regime (20 C) were almost black. My own observations are generally in agreement with this, though average temperatures must be considerably cooler than 20 C before the same effect becomes noticeable in populations from Canada. It is likely that variation in the shade of the green portions on mature larvae is influenced by light intensity as well as by temperature.

The color of the segmental spots on mature larvae is consistent on individuals, but many larval populations are composed of discrete color classes with few intermediates. Clarke and Knudsen (1953) were the first to study the genetic mechanism controlling spot color, by crossing yellow-spotted *P. polyxenes* larvae with orange-spotted *P. machaon* larvae, to produce orange-spotted hybrids. Clarke and Sheppard (1955b,1956a) later showed that the hybrid larvae had spots which were a paler orange than those of *P. machaon*, and although yellow is recessive to orange, the degree of dominance of the orange allelomorph varies with the subspecies of *P. machaon*. They suggested that inheritance was controlled by more than one allele which could produce orange spots, or through modifiers on another locus. Clarke *et al* (1977) established that the main locus controlling larval spot color was not linked to the locus controlling black and yellow wing morphs in adults.

P. machaon, *P. zelicaon*, *P. polyxenes* and *P. indra* are to some extent all polymorphic for larval spot color. Thus, this polymorphism probably predates the most recent common ancestor of these species. Nonetheless, differences in spot color have been used to support some taxonomic distinctions. For example, Remington (1968a) considered the fact that he had found and reared only yellow-spotted larvae of *P. gothica* as evidence contributing to his decision to name it as a separate species. Unfortunately, his sample was comprised of only about ten independent observations and provided little support for his decision when it was considered that most populations of *P. zelicaon* were known to produce both yellow and orange spotted larvae (Clarke and Sheppard, 1970). My observation of 35 larvae with only yellow spots at Gothic (Table 19) provides confirmation of Remington's observation of apparent allelic homogeneity at the locality. It would be interesting to determine if this is generally true of *P. zelicaon* from this region and if the proportion of yellow alleles decreases in populations farther away from *P. polyxenes*.

4.3.2 Spot color in western Canada

Many samples from single localities contained a mixture of both yellow-spotted and orange-spotted larvae, but there were also a number of interesting frequency shifts between different taxa and between different region (Figures 23-24, Table 19).

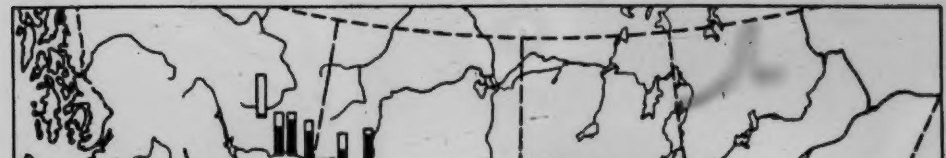
The largest differences in frequency of spot color occurred within *P. machaon*. All of the larvae collected on *Artemisia dracunculus* in southern and central British Columbia had yellow spots, while in southern Alberta and Saskatchewan they almost all had orange spots. Thus *P. m. dodi* and *P. m. oregonius* have undergone a complete allele substitution over much of their range in western Canada. It is not known what the predominant spot color is where these races contact each other in the western United States.

In the Peace River region about one quarter of the larvae of *P. m. pikei* had yellow spots. If spot color is controlled by a single gene with the orange allele dominant

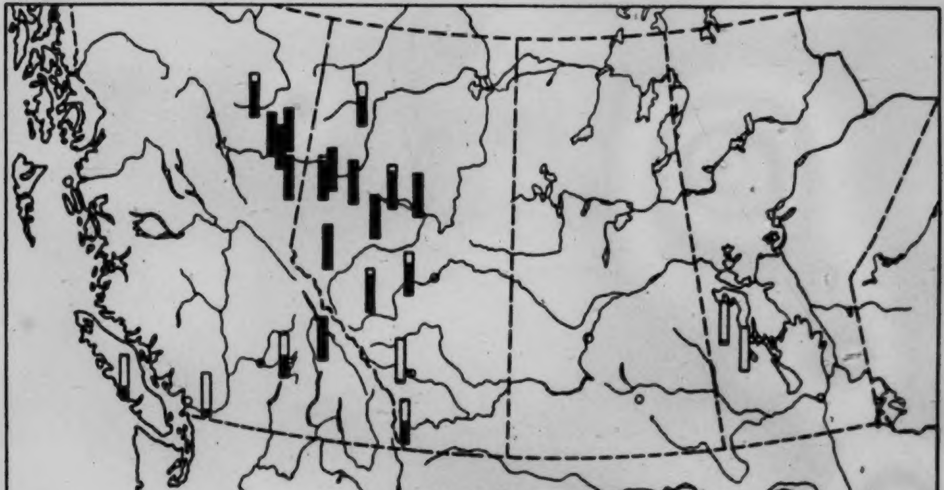
Figures 23 to 24. Frequencies of spot color in larvae of the *P. machaon* group in western Canada. Dark areas of histograms indicate orange or red spots, and light areas indicate yellow spots.

Figure 23. Spot colors of larvae collected on composites. Histograms with broken borders indicate small sample sizes.

Figure 24. Spot colors of larvae collected on umbellifers.



23



24

over yellow, then the Peace River *A. dracunculus*-feeding populations actually have a 50:50 ratio of these two alleles, making them exactly intermediate between *P. m. dodi* and *P. m. oregonius*.

There were far more yellow-spotted larvae in *P. m. aliaska* than in *P. m. pikei*, since more than 90% of the larvae collected on *A. arctica* had yellow spots. The single larva of *P. m. hudsonianus* which was scored (from a photograph by G. Anweiler) also had yellow spots. Thus *P. machaon* is clearly polymorphic for spot color in North America, but different ecological and geographic races have major frequency differences in spot color.

Almost all the locality samples of larvae collected on umbellifers in Alberta and British Columbia were polymorphic for spot color. Hence geographically separate populations of *P. zelicaon* and its hybrids may have quite different frequencies of spot color, as in *P. machaon*. However, the frequency shifts seem to be somewhat more clinal. Also, *P. zelicaon* larvae consistently had different spot color frequencies from *P. machaon* where these species have low hybridization rates. In Interior British Columbia and the Peace River region, *P. zelicaon* larvae had more orange spots, while in southern Alberta they had more yellow spots. This trend was maintained even when the larvae were collected within easy adult flying distance of each other, as at Pink Mountain and Hudson Hope (Table 19).

Hybrid populations did not show much difference from parent species. In central Manitoba, most of the larvae had yellow spots, while *P. polyxenes* larvae generally have yellow spots farther to the southeast, and the only known larval *P. m. hudsonianus* also had yellow spots. In central Alberta the northern populations have mostly orange spots and in this respect merge into the *P. zelicaon* populations farther to the north and west. This trend is mirrored in the adult morphometric and electrophoretic characters of these populations.

The shift toward predominantly yellow spots in the *P. zelicaon X machaon* hybrid swarm west of Calgary is more abrupt, however. Also, it is interesting to note that the only larva found on *Heracleum* at Bragg Creek had orange spots, while two of 44 on *Zizia* had yellow spots. *Heracleum* is a much more common larval foodplant for *P. zelicaon* populations immediately to the west, and so the larva on this foodplant may have been oviposited by a typical *P. zelicaon* that strayed in from the west. The fact that *P. m. dodi* larvae almost always have orange spots, even at the outer edges of the range of this subspecies, distinguishes the latter from the southern hybrid populations. This supports the contention that the hybrid populations are the result of hybridization of *P. zelicaon* with races similar to *P. m. husonianus*, rather than with *P. m. dodi*.

5. ECOLOGICAL CHARACTERISTICS

5.1 Taxonomic Distinctions

5.1.1 Geographic distribution and habitat

The *Papilio machaon* group has a generally Holarctic distribution. Of the eight species recognized, two occur only in western Eurasia and four are restricted to North America (Table 10). Of the two Eurasian endemic species, *P. alexanor* is the most primitive member of the species group, while *P. hospiton* shows clear phylogenetic affinities with *P. machaon* (ref. later chapter on phylogeny).

The western United States and Canada are the only part of the range of the *P. machaon* group in which there is extensive sympatry between species. All other regions support only a single species, or a contact zone between two species which is maintained in part by habitat segregation. For example, *P. polyxenes* is separated by habitat from other species in several parts of its range. In areas in Atlantic Canada where the two species are parapatric, *P. polyxenes* is generally found inland in agricultural areas, while *P. brevicauda* is found close to the ocean (Ferguson, 1954). In Colorado, *P. polyxenes* occurs at lower altitudes than *P. zelicaon*, though these two species meet and occasionally hybridize along a broad zone of contact (Remington, 1968b; Fisher, 1980; Scott, 1981). In Missouri, *P. polyxenes* completely surrounds the range of *P. joanae*, and apparently these two species are reproductively isolated, in part by habitat preferences (Heitzman, 1973). However, *P. polyxenes* and *P. joanae* are distinguished by very few morphological characteristics, and though *P. joanae* is recognized as a distinct species in popular works such as Opler and Krizek (1984), the contention of isolation is clearly in need of confirmation.

The species of the *P. machaon* group which have broad ranges also show a considerable diversity of habitat preferences. For example, different populations of *P. machaon* have adapted to habitats varying from cool temperate wetlands to hot deserts (Table 10). The ecological flexibility of *P. machaon* is illustrated by the races in Nepal, of which one is adapted to drylands above the continuous cloud belt, and is distinct from a wet monsoon-forest adapted race below the cloud belt (Dierl, 1976). Such lability of habitat association may occur with relatively little evidence of regional morphological differentiation, as in mountain versus prairie-adapted populations of *P. zelicaon*.

Three species of the *P. machaon* group occur in western Canada: *P. machaon*, *P. zelicaon* and *P. polyxenes*. These species interact in a complex pattern of geographic overlap, replacement along contact zones, and varying frequencies of hybridization (Table 11).

P. machaon has five subspecies in western Canada, and is the only species in this area which is represented by more than one subspecies. The subspecies of *P. machaon* are all either allopatric with each other, or paratric but with very limited opportunities for gene flow (Figure 26). *P. m. hudsonianus* is rare in northern Alberta and northwestern Saskatchewan (eg. Bird *et al*, 1982), and there is little opportunity for contact with either *P. m. aliaska* or *P. m. pikei* (Figures 25 and 26). *P. m. dodi* and *P. m. oregonius* are separated from the northern subspecies and, in Canada, from each other.

Papilio machaon has adapted to most of the available major vegetation zones in western Canada (Table 10, Figure 30 and 31). This can be shown by relating long term records for temperature and precipitation (Canadian Climate Normals, 1951-1980. [1982a and 1982b]) for weather stations close to localities at which specimens have been collected. These show a clear pattern of habitat segregation among the subspecies of *P. machaon*, as well as between *P. machaon* and the other two species (Figure 32 and 33).

P. m. dodi, *P. m. oregonius* and *P. m. pikei* are most common in patchy populations in dry valley bottoms and slopes of river banks or badlands. They are replaced by *P. zelicaon* at higher altitudes and in moister habitats (eg. McDunnough, 1927), though males of the two species are occasionally collected together on hilltops immediately surrounding dry valleys. *P. m. aliaska* is replaced by *P. zelicaon* in forested areas south of the Peace River, although *P. zelicaon* is not a resident in alpine habitats

Table 10. Habitats and ranges of *P. machaon* group taxa

References are given for regions and taxa which are outside of western Canada and which I am not familiar with.
Abbreviations: BC=British Columbia, AB=Alberta, SK=Saskatchewan, w.=west, e.=east, s.=south, n.=north. Can.=Canada

	Habitat	Range
P. alexanor	dry mountainous areas to more than 1000 m (Higgins & Riley, 1970; Nakamura & Ae, 1977)	southern France to Iran & Turkestan
P. hospiton	mountainous areas to more than 1000 m (Kettlewell, 1955; Higgins & Riley, 1970)	Corsica and Sardinia
P. machaon, Eurasian ssp.	highly variable, eg. wetlands (Wiklund, 1974a; Dempster and Hall, 1980), Saharan desert oases (Larson, 1980),	almost entire Palearctic region upland tundra/taiga (Kurentzov, 1970).
P. m. aliaska	alpine tundra, occasional in boreal forest	n. AB to Quebec
P. m. hudsonianus	boreal forest, especially stoney muskeg	Alaska to n. BC and w. Northwest Terr.
P. m. pikei	dry, eroding clay slopes in parkland	n.e. BC and n.w. AB
P. m. oregonius	dry slopes in bunchgrass prairie (Dornfeld, 1980)	s. BC interior, n.w. United States
P. m. dodi	disturbed slopes in shortgrass or fescue prairie	s. AB & SK, n. plains United States
P. m. bairdii	Upper Sonoran Zone (Fisher, 1980)	Colorado & s. Utah to s.e. California
P. zelicaon X *machaon*	boreal forest or mixed montane forest	west-central Alberta
P. zelicaon X *machaon*	mixed montane forest	s.e. AB and s.w. SK (Cypress Hills)
P. zelicaon (in w. Can.)	wet lowlands to subalpine forest	s. and central BC
P. zelicaon (in w. Can.)	parkland hills to subalpine forest	n.e. BC and n.w. AB
P. zelicaon (in w. Can.)	prairie hills to subalpine forest	s. AB and s.w. SK
P. zelicaon	range of habitats, esp. mountainous regions (Emmel and Emmel, 1973; Fisher, 1980)	all of w. United States to Baja Calif.
P. polyxenes X *machaon*	white spruce or mixed forest	central Manitoba and east-central SK
P. p. asterius (w. Can.)	aspen parkland, usually on agricultural land	s. and central Manitoba, s.e. SK
P. p. asterius	wide range of open habitats (Opler & Krizek, 1984)	e. Canada and United States, n. Mexico
P. p. coloro	desert (Emmel & Emmel, 1973; Ferris & Emmel, 1982)	Arizona & s.w. Utah to s.e. California
P. p. polyxenes	open habitats as for *P. p. asterius* (Riley, 1975)	Cuba
P. p. stabilis	disturbed openings in forests (Blau, 1981b)	Central America
P. p. americus	drier habitats at 1800-3000 m (Brown, 1953)	Venezuela, Colombia, Ecuador, n. Peru
P. joanae	thickly wooded highlands (Heitzman, 1973; Opler & Krizek, 1984)	Missouri Ozarks
P. brevicauda	seashores and cliffs (Ferguson, 1954; Jackson, 1981)	Maritime region of e. Canada
P. indra	dry, rocky canyons (Emmel and Emmel, 1973; Dornfeld, 1980; Fisher, 1980)	all of w. United States

Table 11. Geographic contact between taxa and frequency of black morphs in western Canada

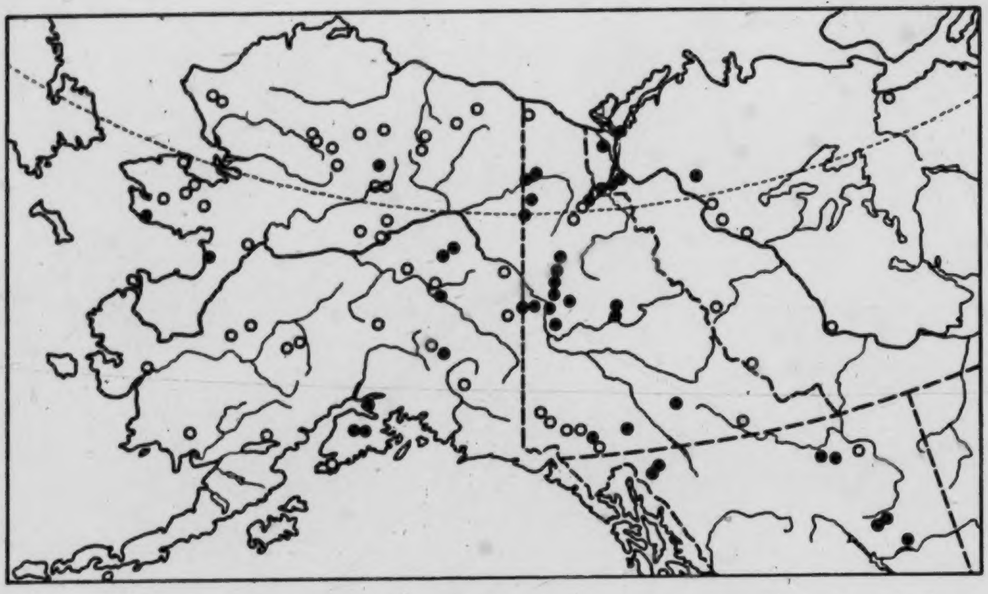
S = sympatry, with habitat segregation
P1 = abrupt geographic replacement, with low frequency of hybrids
P2 = low density contact zone between populations
P3 = clinal merging of populations
A = allopatry, with disjunction of more than 100 km

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	Black Morph
1. *P. m. aliaska*												0
2. *P. m. hudsonianus*	P2											0
3. *P. m. pikei*	P1	P2										0
4. *P. m. oregonius*	A	A	A									0
5. *P. m. dodi*	A	A	A	A(P3 in western U.S.)								2%
6. *P. zelicaon* X *machaon* -central Alberta	A	P2	A	A	P1							0(north) to 12%(south)
7. *P. zelicaon* X *machaon* -Cypress Hills	A	A	A	A	P1	A						approx. 12%
8. *P. zelicaon* -southern British Columbia	A	A	A	S	A	P1	A					0
9. *P. zelicaon* -Peace River region	P1	P2	S	A	A	P3	A	P3				0
10. *P. zelicaon* -southern Alberta & Sask.	A	A	A	A	S	P1	P3	P3	P2			5-15%
11. *P. polyxenes* X *machaon* -central Manitoba	A	S	A	A	A	A	A	A	A	P2		approx. 97%
12. *P. p. asterius*	A	P1	A	A	P2	A	A	A	A	P2	P3	100%

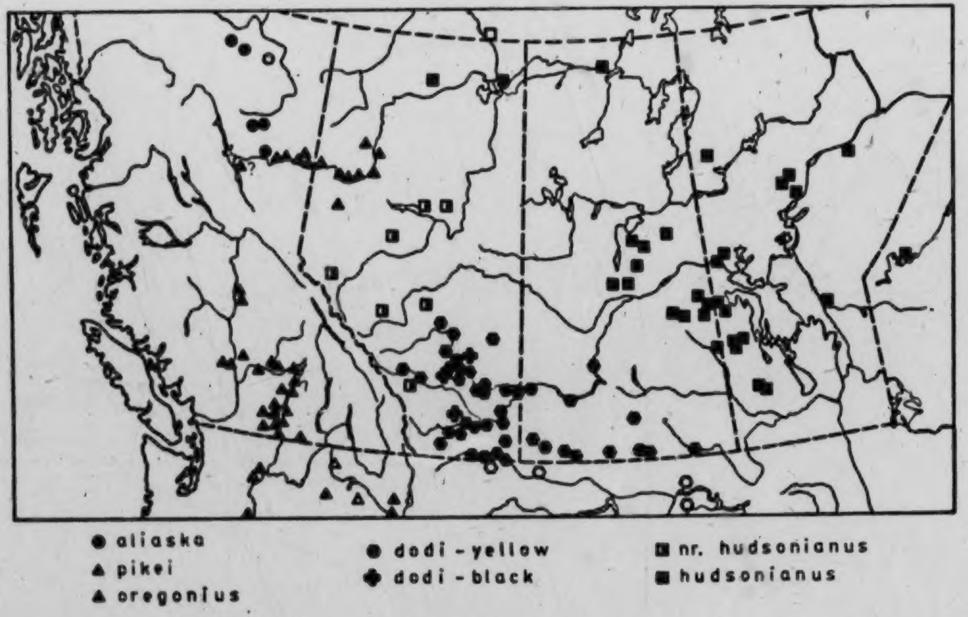
Figures 25 to 26. Empty symbols indicate unverified published records.

Figure 25. Distribution of *P. m. aliaska*.

Figure 26. Distribution of *P. machaon* in western Canada.



25

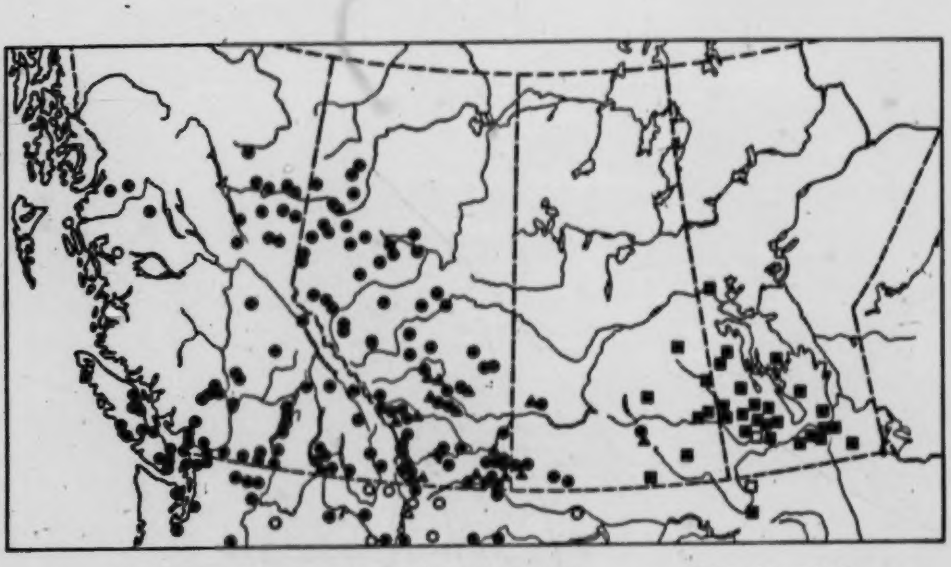

● aliaska
▲ pikei
▲ oregonius
● dodi - yellow
✚ dodi - black
▣ nr. hudsonianus
■ hudsonianus

26

Figures 27 to 28.

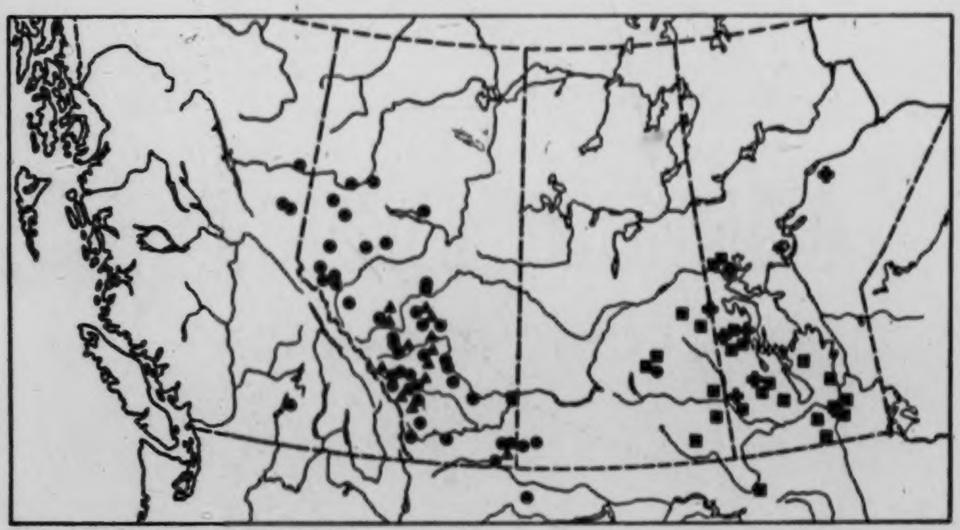
Figure 27. Distribution of *P. zelicaon* and *P. p. asterius* in western Canada. Empty symbols indicate unverified published records.

Figure 28. Distribution of interspecific hybrids in western Canada.



● zelicaon - yellow ▲ zelicaon - black ■ polyxenes

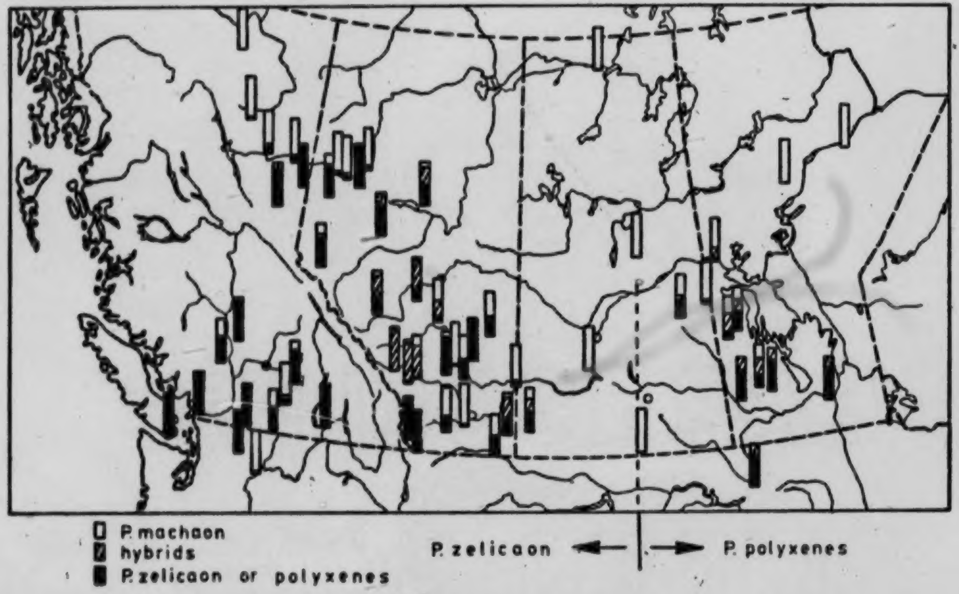
27



● zelicaon X machaon - yellow ✚ machaon X polyxenes - yellow
▲ zelicaon X machaon - black ■ polyxenes X machaon - black

28

Figure 29. Frequency of interspecific hybrids in western Canada.


▯ P. machaon
▨ hybrids
▮ P. zelicaon or polyxenes
P. zelicaon ←
→ P. polyxenes

29

Figures 30 to 31.

Figure 30. Major vegetation zones in western Canada.

Figure 31. Mean annual temperature and precipitation of major vegetation zones. Canadian Climate Normals, 1951-1980 (1982a and 1982b).

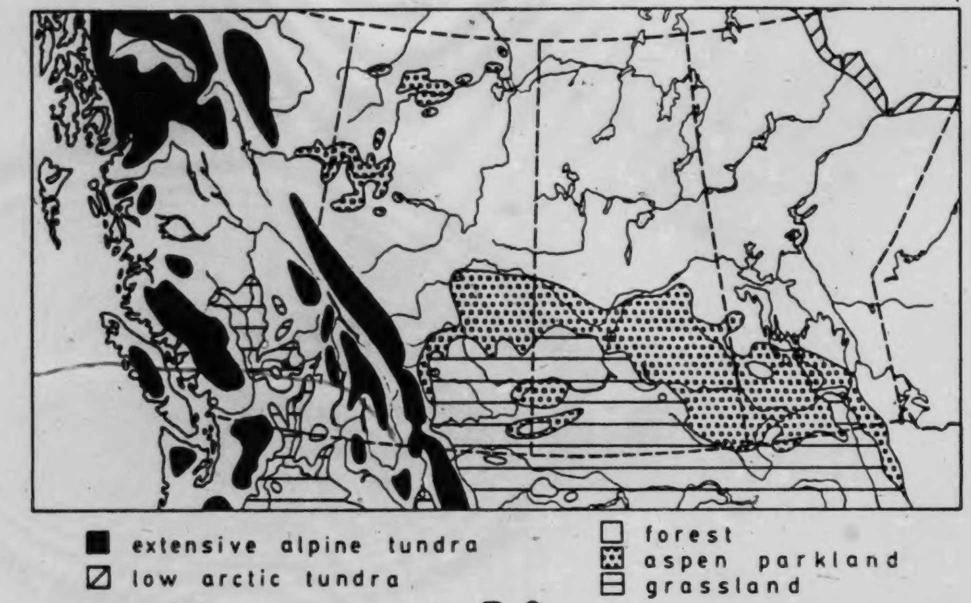
1. Grassland in southern British Columbia (BC)
2. Grassland in southern Alberta and Saskatchewan
3. Aspen parkland of Alberta to Manitoba

4a. Boreal forest of northern BC to Quebec

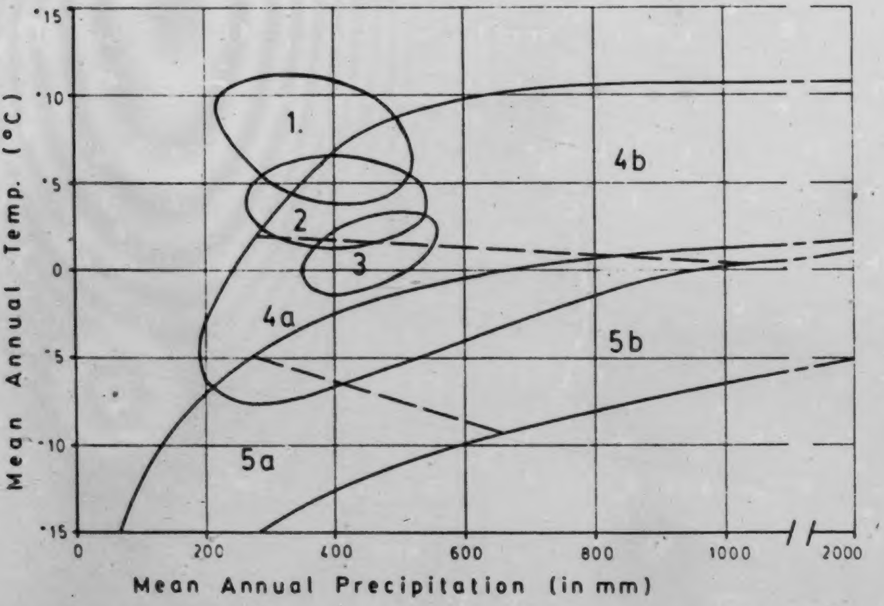
4b. Forest of south and central BC

5a. Arctic tundra of Northwest Terr. to Quebec

5b. Alpine tundra of Alberta, BC and Yukon


■ extensive alpine tundra
▨ low arctic tundra
☐ forest
▩ aspen parkland
☰ grassland

30


Mean Annual Temp. (°C)
15
10
5
0
-5
-10
-15
Mean Annual Precipitation (in mm)
0
200
400
600
800
1000
2000
1.
2
3
4a
4b
5a
5b

31

Figures 32 to 33.

Figure 32. Occurrence of *P. machaon* subspecies vs. mean annual temperature and precipitation.

1. *P. m. oregonius* in southern British Columbia
2. *P. m. dodi* in southern Alberta and Sask.
3. *P. m. pikei*

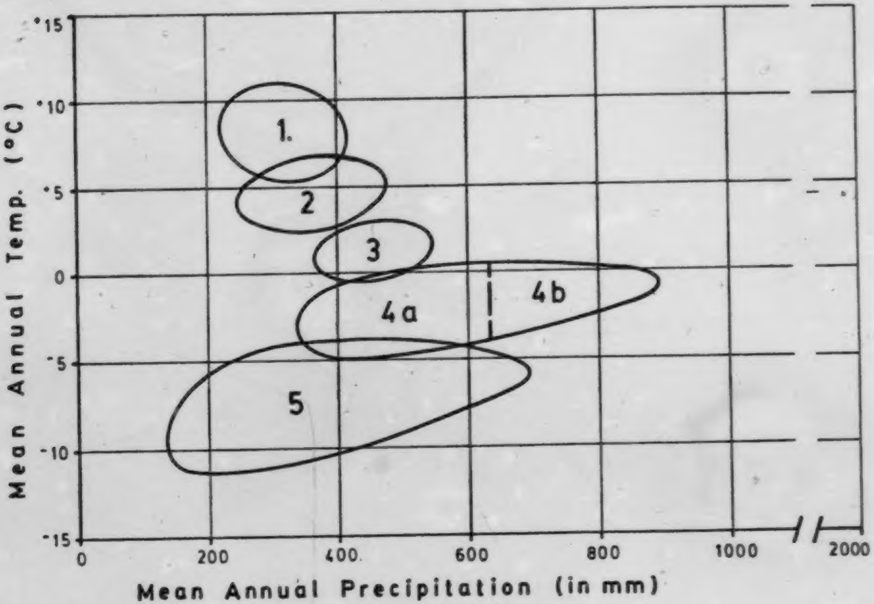
4a. *P. m. hudsonianus* in Alberta to Manitoba

4b. *P. m. hudsonianus* in Ontario and Quebec

5. *P. m. aliaska*

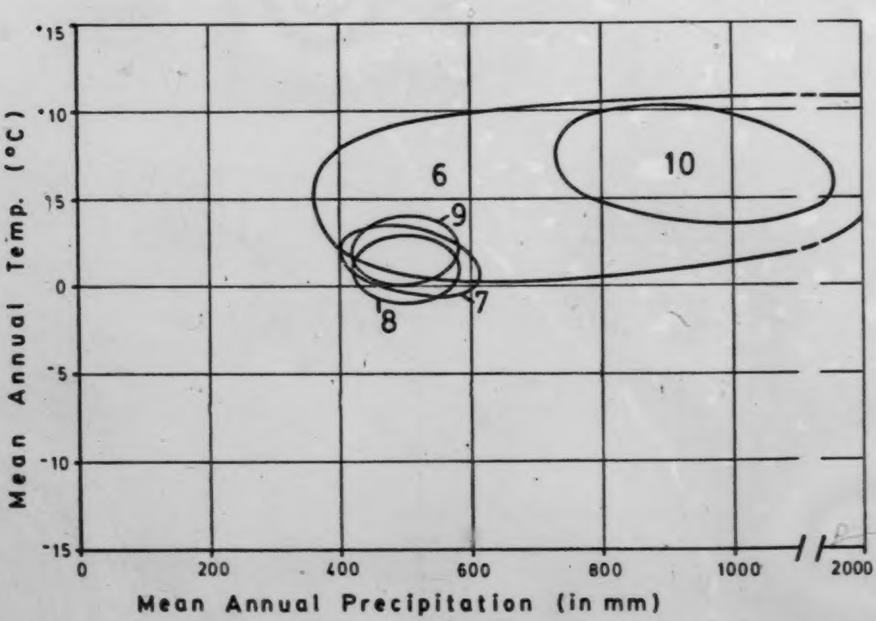
Figure 33. Occurrence of *P. zelicaon* and *P. polyxenes* vs. mean annual temperature and precipitation.

6. *P. zelicaon* in Alberta and British Columbia
7. *P. zelcaon* X *machaon* in central Alberta
8. *P. polyxenes* X *machaon* in central Manitoba
9. *P. p. asterius* in southern Manitoba
10. *P. p. asterius* in eastern Canada



+15
+10
+5
0
-5
-10
-15
Mean Annual Temp. (°C)
0
200
400
600
800
1000
2000
Mean Annual Precipitation (in mm)
1.
2
3
4a
4b
5

32



+15
+10
+5
0
-5
-10
-15
Mean Annual Temp. (°C)
0
200
400
600
800
1000
2000
Mean Annual Precipitation (in mm)
6
9
7
8
10

33

and only a few individuals fly to the tops of the lower mountains. Freeman's (1972) report that northern populations of *P. machaon* are not found in areas with acidic granitic formations seems unlikely, since *P. m. hudsonianus* is most common in habitats dominated by black spruce, which are often acidic, and northern Manitoba, which has few sedimentary formations.

In contrast to the situation within *P. machaon*, populations of *P. zelicaon* are relatively continuous, with no evidence of any major disjunctions within the species (Figure 27). *P. zelicaon* occurs in broad sympatry with *P. machaon* over most of western Canada, with a frequency of less than 5% of natural hybrids (Figure 29).

Although *P. zelicaon* hybridizes with *P. m. dodi* only rarely over most of its range, these two species have formed a hybrid population in the Cypress Hills of southeastern Alberta and southwestern Saskatchewan (Figure 28 and 29). *P. zelicaon* is found on the partially wooded and prairie hills surrounding the plateau, sometimes together with *P. m. dodi*, but both species merge into a hybrid population in the more heavily wooded central areas. Distinguishing the forms in the Cypress Hills is difficult, since electrophoretic data are not available. However, a number of females have been collected in the more central parts of the Cypress Hills, and none were from habitats likely to contain any *Artemisia dracunculus* suitable for oviposition by *P. m. dodi*. Since females in the *P. machaon* group are usually found close to habitats in which larval foodplant grows, these individuals are unlikely to be *P. m. dodi*. On the other hand, they all have connected anal pupils and most have thick streaks of yellow scaling in the disc of the VFW, and so they differ from the *P. zelicaon* adults found on the prairie hills surrounding the Cypress Hills. The "Cypress Hills Old World Swallowtail" (misidentified as *P. m. dodi*) of Hooper (1973), most likely refers to this hybrid swarm material.

There is a much larger series of hybrid populations in central Alberta, which are probably the result of genetic swamping of a *P. m. hudsonianus*-like population which once existed in this region (Figure 43 and 45). *P. zelicaon* abruptly replaces the hybrid swarm populations west of the easternmost slope of the Rockies in Alberta, as well as south of the Crowsnest Pass. Near Lesser Slave Lake, at the northern edge of the central Alberta hybrid swarm, hybrid specimens form 20-40% of the total population at any one locality. This frequency increases toward the south and reaches a maximum west of Calgary, where specimens assigned as hybrids comprise more than 90% of the total populations (Figure 29). I have noticed no difference in habitat between individuals which are the most *P. zelicaon*-like, and those which are the most *P. machaon*-like ("nr. *hudsonianus*" in Figure 26), and there is in fact not much habitat variation in this predominantly boreal and montane forest region which would allow the two species to occupy different niches. Almost all the localities at which hybrid populations can be found occur between 1000 and 2000 m elevation in central Alberta, while localities recorded for *P. m. dodi* are below 1100 m (Figure 11). Hybrid forms are less common farther south and east of Calgary, probably because the foothills and mixed forest habitat they occupy is greatly reduced in extent. South of the Crowsnest Pass in southern Alberta, grassland extends to the base of the Rocky Mountains and hybrids appear to be absent. There are a few hybrid specimens from Bragg Creek and Buck Lake, which seem likely to have been derived in part from *P. m. dodi*. These adults have the long tails and pointed forewings which usually distinguish *P. m. dodi* from *P. m. hudsonianus*.

P. polyxenes occurs in only the southeastern portion of western Canada (Figure 27), where the species fills part of the gap between boreal *P. m. hudsonianus* and prairie *P. m. dodi* and *P. zelicaon* (Figure 29). *P. polyxenes* X *machaon* populations from central Manitoba occupy a habitat very similar to that of *P. zelicaon* X *machaon* populations from central Alberta (Figure 33). Because some *P. polyxenes* X *machaon* individuals are very difficult to distinguish from typical *P. p. asterius* individuals, Figure 27 probably represents an overestimation of the extent of the range of *P. p. asterius* in central Manitoba, and the same for hybrids in southern Manitoba (Figure 28). *P. p. asterius* is very uncommon in southern Saskatchewan, and so there is little contact with *P. zelicaon*.

The hybrid populations in central Manitoba are for the most part isolated from the main range of *P. m. hudsonianus* and may be in the process of being swamped by *P. polyxenes* in the area, along with the remnants of *P. m. hudsonianus*. Most typical *P. m. hudsonianus* adults were collected in Riding Mountain Park in the 1930's and 1940's, at which time they appeared to form about half of the catch of local collectors. By 1955 *P. m. hudsonianus* was already quite uncommon (Remington, 1956), and in the mid 1970's it was certainly very rare (Heron and Robinson, 1976). Intermediate black morph adults also may be becoming less common, since they were at least as common as more typical *P. polyxenes* in the 1930's to 1950's, but have formed a lower proportion of the total catch in the last two decades. As well, specimens closer to the typical appearance of *P. p. asterius* are more common in the farmland around the central plateaus, which surrounds Riding Mt. Park completely and Duck Mt. Park on three sides. The changing status of the hybrid populations in central Manitoba is a major reason for retaining the established taxonomic practice of recognizing these taxa as separate species.

5.1.2 Phenology

Variation in flight period and voltinism in the *Papilio machaon* group is comprised primarily of geographic variation within species. *P. machaon*, *P. zelicaon*, and *P. polyxenes* each include a variety of different populations which range from strict univoltinism to multivoltinism, and have a flight period for adults which ranges from a few weeks per year to an almost or completely continuous emergence (Blau, 1981a, 1981c; Dornfeld, 1980; Emmel and Emmel, 1973; Fisher, 1980; Wiklund, 1973; Wiltshire, 1958). The remaining species in the *P. machaon* group also have fairly flexible phenologic characteristics. Some populations of *P. indra* and *P. hospiton* are partially bivoltine (Fisher, 1980; Kettlewell, 1955). These two species and *P. alexanor* may have a very extended emergence period, depending on climatic conditions, and some pupae of *P. indra* and *P. alexanor* can remain in diapause for several years (Fisher, 1980; Nakamura and Ae, 1973). Since most species in the *P. machaon* group exhibit labile phenologic responses to different habitats, the genetic potential to adjust in these ways is probably plesiotypic within the species group, and so does not indicate any monophyletic lineages.

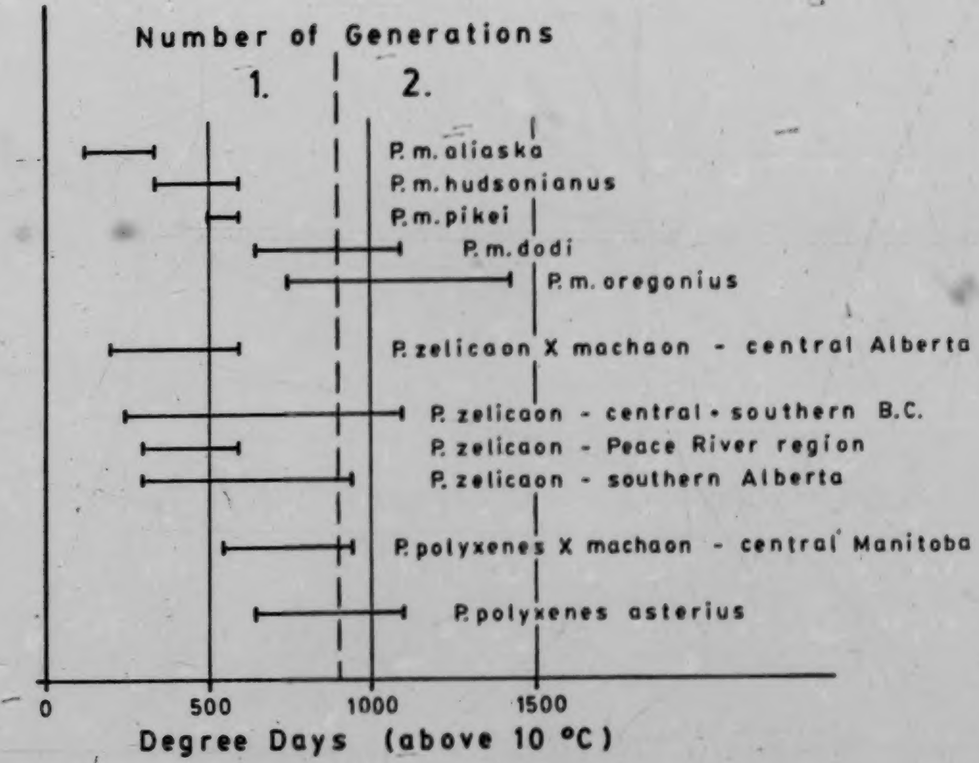
Phenologic variation in *P. machaon* group species is less pronounced in western Canada (Table 12), due to a more limited range of habitats. *P. machaon* and *P. zelicaon* are strictly univoltine in the northern regions of western Canada, and have a large second generation in the warmer southern regions (Figure 34). Bivoltinism is more widespread in southern *P. machaon* than in *P. zelicaon*, probably because the *P. machaon* populations occupy warmer habitats. *P. polyxenes* is at least partly bivoltine through most of its range in western Canada, but also shows a marked decrease in

Table 12. Flight periods in western Canada

X = peak, + = reduced numbers, - = rare.

Taxon	April				May				June				July				August				September			
P. machaon aliaska								-		+	X	X	X	X	+	-		?	?					
P. machaon hudsonianus							-	-	-	+	X	X	X	+	-	?								
P. machaon pikei										X	X	X	+	+							?			
P. machaon dodi					-	+	X	X	X	+	+	+	-	-	+	+	X	-	-					
P. machaon oregonius			-	-		-	+	+	-	-	-	-	-	+	X	X	+	+	-					
P. zelicaon X *machaon* - central Alberta							-	+	X	X	X	+	+	+	-	-	-							
P. zelicaon X *machaon* - Cypress Hills							-	-		-	+	+	X	+	-			-						
P. zelicaon - southern British Columbia	-	-	-	+	+	-	X	+	+	+	+	X	+	+	+	-	-	-		-	-	-		
P. zelicaon - Peace River region										+	X	+	+	+										
P. zelicaon - southern Alberta prairie					-	+	+	X	-	-				-	-			-	-					
P. zelicaon - southern Alberta mountains					?	?				-	-	X	X	+	-	-	-	-	-					
P. polyxenes X *machaon* - Manitoba						-	-	-	+	X	X	X	+	-	-	-	-	-	-					
P. polyxenes asterius - Manitoba							+	+	X	X	X	+	-	-	+	+	-	-	-					
Bragg Creek: nr. *P. machaon*									-	+														
P. zelicaon X *machaon*							-	+	X	X	X	+	-	-			-							
nr. *P. zelicaon*								-	+	+	-	-	-	+	-	-	-	-	-					

Figure 34. Relationship between voltinism and degree days. Bars show range of degree days (above +10 C) to which *P. machaon* group taxa are exposed in western Canada. Data are taken from weather stations near collection localities (Canadian Climate Normals, 1951-1980. [1982c]). Dashed line indicates approximate number of degree days above which populations have a partial second brood.



Number of Generations
1.
2.
P. m. aliaska
P. m. hudsonianus
P. m. pikei
P. m. dodi
P. m. oregonius
P. zelicaon X machaon - central Alberta
P. zelicaon - central • southern B.C.
P. zelicaon - Peace River region
P. zelicaon - southern Alberta
P. polyxenes X machaon - central Manitoba
P. polyxenes asterius
0
500
1000
1500
Degree Days (above 10 °C)

34

the size of the second generation toward the north, even though it occupies the relatively warm agricultural areas. The main flight period tends to occur slightly later in the year at higher altitudes and latitudes for all three species.

Although *P. zelicaon* adults tend to emerge slightly earlier in the season than those of *P. machaon* where these species are sympatric, the amount of overlap in flight period is still very large and cannot account for any interruption in gene flow between the species. The same applies to the flight periods of *P. machaon* and *P. polyxenes* in Manitoba.

Voltinism of *P. machaon* group populations is related to growing temperatures in western Canada. Figure 34 shows the approximate range of degree days above 10 C (Canadian Climate Normals, 1951-1980. [1982c]) to which these different populations are exposed. Populations which have some adults emerging in a second brood occur in areas receiving approximately 900 or more degree days per year. This contrasts with the situation in *P. glaucus*, in which the potential for multivoltinism appears in populations from areas receiving more than 1200 degree days per year (Scriber, 1982).

Despite similarities among related species with respect to voltinism and adult emergence, many artificial hybrids show unusual characteristics of pupal diapause which are not present in parental species. Such unusual characteristics can be relatively pronounced when both species are within the same species group (as are *Papilio glaucus* L. and *P. rutulus* Lucas [Clarke *et al*, 1972]), as well as when they are more distant, as are *Papilio machaon* and *P. xuthus* (Shimada, 1979). Within the *P. machaon* group, Oliver (1969) showed that hybrids of *P. polyxenes* and *P. zelicaon* have no pupal diapause under the long day conditions that cause at least some proportion of the parental species to undergo diapause. However, under short day conditions, all the hybrid pupae underwent diapause, just as did almost all the pupae of the parental species.

Adult hybrids of *P. machaon* and *P. zelicaon* from areas where natural hybrids are rare usually fly at the same time as the main flight of the species with which they are found. There are interesting exceptions to this in the grasslands of both the Peace River region and southern Alberta, where the latest record for any *P. machaon* group individual is for a hybrid specimen. Hence, it is likely that the natural mixing of two different gene pools occasionally produces individuals with characteristics different from either parent, much as in artificial hybrids.

As in the situation where hybrid individuals are rare, most hybrid populations do not show any unexpected phenological characteristics, probably because any genetic incompatibility that existed between the parental species when the hybrid populations were being formed has since been eliminated by selection. For example, in central Alberta the most *P. machaon*-like and the most *P. zelicaon*-like individuals generally fly in about the same proportions through most of the flight period.

An interesting exception to this occurs at Bragg Creek, where *P. zelicaon*-like individuals occur at low frequency throughout the flight period, but include the only two specimens collected as late as mid August (Table 12). The most likely explanation for the occurrence of these individuals is that they have dispersed in from the more typical *P. zelicaon* populations in the mountainous Kananaskis area immediately to the west. As well, most of the *P. zelicaon* adults west of Bragg Creek fly at least a month later than hybrid populations, though they seem to stray eastward occasionally late in the summer. The partial isolation of these hybrid populations is a further reason for treating them separately from the parental species.

Another exception occurs in central Manitoba, where some black morph individuals of *P. polyxenes* X *machaon* have been collected during the second brood flight period, but yellow morph hybrid individuals are only known from the first brood. No second brood individuals are known for typical *P. m. hudsonianus* either.

The *P. zelicaon X machaon* hybrid populations in the Cypress Hills of southeastern Alberta and southwestern Saskatchewan appear to have a flight period which is more consistently distinct from that of the parental species in the surrounding areas (Table 12). The difference in flight period may in part be due to a lower mean temperature during the growing season on the Cypress Hills. Adults may fly much earlier and later in the year on the partially forested outskirts of the hills, and it is concievable that there is a continuous low rate of hybridization of the parental species along the edge of the forested areas, both in the first and second generations. However, some genetic differentiation and adaptation has probably also occurred in the central hybrid populations, since these populations tend to fly even later than do the *P. machaon* group populations at similar altitudes in the foothills of the Rocky Mountains immediately to the west and northwest.

The considerable variation within *P. machaon*, *P. zelicaon* and *P. polyxenes* in phenologic characteristics contributes to the formation of a variety of ecological races in these species. This variation grades clinally from one region to another and is generally not useful for making taxonomic distinctions, even at the subspecies level.

P. m. pikei is an exception to this. It is distinguished from southern *A. dracunculus*-feeding *P. machaon* subspecies by that some proportion of these southern populations emerges as a second generation both in the wild and when reared in the laboratory, while *P. m. pikei* is strictly univoltine. Also, adults of *P. m. pikei* emerge a relatively long time after the onset of warm temperatures, compared to *P. m. dodi*, *P. m. oregonius* and *P. m. aliaska*. Diapause termination in *P. m. pikei* is unusual among the subspecies of *P. machaon*, because it requires both a long photoperiod and a period of cool temperature. Of 128 reared adults, none emerged without a cool period of at least 50 days, and a high proportion did not emerge unless the pupae were exposed to at least 17 hours of light per day. All other samples of *P. machaon* which I have reared emerged at high frequencies at shorter light periods, probably because they tend to emerge much earlier in the growing season in their natural habitats. These differences probably are to some extent due to genetic differences, since they remain even when pupae and late instar larvae of the different subspecies are subjected to the same rearing conditions.

Some forms in wing pattern are probably the result of an interaction between unusual temperature conditions and a genetic predisposition to a particular aberration in wing pattern. The form *mcdunnoughi* Gunder (1928), was described in *P. zelicaon* from Waterton, Alberta, and individuals similar to the type specimen are still occasionally collected in the area. The form is characterized by unusually broad submarginal black bands on the fore and hind wings. I have obtained a number of such specimens from reared stock of *P. zelicaon* collected in Waterton Park in 1981. I also have reared one specimen of *P. m. dodi* from Drumheller which approaches the form. It seems likely to me that the expression of the form is dependent on the larvae being exposed to unusual temperature conditions late in the fifth instar. The Waterton larvae were accidentally exposed to temperatures high above 35 C, while the Drumheller specimen pupated at about 5 C.

5.1.3 Larval foodplants

Larvae of the *P. machaon* group feed on a wide variety of species of Umbelliferae, Rutaceae and Compositae. Umbellifers are the most commonly recorded foodplants, though most species can feed opportunistically on rutaceous plants, and some populations of *P. machaon* have switched to composites. Within a restricted area, however, most larvae of a species are only found on one or a few species of foodplant.

The ability to feed on rutaceous plants is widespread in the Papilioninae, and particularly in the genus *Papilio* (Ehrlich and Raven, 1964; Richard and Guedes, 1983). Umbellifer-feeding species are restricted to *Papilio*, and are concentrated in the *P. machaon* group. Umbellifer-feeding habits outside the *P. machaon* group are found in larvae of *Papilio demodocus* Esper and a few species of the *Papilio thoas* L. group (Monroe, 1961), though none of these species have umbellifers as major hostplants. On the other hand, the composite-feeding habits of *P. machaon* larvae are unique within the Papilionidae. Thus the composite-feeding habit is clearly the most derived trait, while the rutaceous-feeding habit is the most ancestral one.

Of the species in the *P. machaon* group, *P. machaon* larvae feed on the greatest range of foodplants. Records for

Eurasian larvae of *P. machaon* are mainly from umbellifers, less commonly on rutaceous plants, and only accidentally on plants of other families. An important exception occurs in Afghanistan, where Müting (1972) found mature larvae of *P. machaon* on "Wermutstrauchern" (*Artemisia absinthium L.*: Compositae) in northeastern Afghanistan. Larvae of *P. machaon* subspecies from North America appear to feed almost exclusively on composites, and particularly on plants of *Artemisia* (Figure 35 and 36). This contrasts with *P. machaon* populations from northeastern Siberia, which often occur in similar habitats, but for which Kurentzov (1970) mentions only a variety of umbellifers as larval foodplants.

The only two records for wild-collected larvae of *P. m. aliaska* from North America are from composites (Table 20). One larval record for *P. m. aliaska* is from *Artemisia arctica* (this study) and the other is from *Petasites palmatus* var. *frigidus* (Leussler and Bryant, 1935). Other foodplant records for *P. m. aliaska* refer to ovipositions observed on *A. arctica* plants. *P. m. aliaska* females frequently investigate *A. arctica* in the wild and oviposit freely on these plants in cages. Females appear to oviposit only on plants from moist sites, with relatively glabrous, bright green leaves, rather than greyer, non-pubescent plants from dry sites, even though samples of both have been identified as *A. arctica* (by J.G. Packer -1981; and A. Rose -1982).

Table 13. Larval foodplants of *P. machaon* group taxa

Abbreviations: umb. = umbellifers, rut. = rutaceous plants, comp. = composites

P. alexanor: variety of umb., esp. *Seseli* (Higgins & Riley, 1970; Larsen, 1974; Nakamura & Ae, 1977)
P. hospiton: umb., esp. *Ferula* (Kettlewell, 1955; Weidemann, 1982)

P. machaon, Eurasian ssp.: mostly umb., many species (eg. 20 species in Sweden -Wiklund, 1974); less common on rut.; also comp. (*Artemisia absinthium* L.) in Afghanistan (Müting, 1974); accidental(?) on Tamaricaceae (Wago, 1973)
P. m. aliaska: comp., esp. *Artemisia arctica* Less., also *Petasites palmatus* (Ait.)Gray (Leussler and Bryant, 1935)
P. m. hudsonianus: one record, on comp. - *Petasites palmatus* (Ait.)Gray
P. m. pikei, *P. m. oregonius*, *P. m. oregonius*, *P. m. bairdii*: only comp. - *Artemisia dracunculus* L.

P. zelicaon X *machaon* (central Alberta): mainly *Heracleum lanatum* Michx. in north, *Zizia aptera* (A.Gray)Fern. in south
P. zelicaon X *machaon* (Cypress Hills): no records, probably mainly *Zizia*

P. zelicaon (south and central British Columbia): variety of umb., esp. *Heracleum* and *Angelica*
P. zelicaon (Peace River region): variety of umb., esp. *Heracleum*
P. zelicaon (s. Alberta): variety of umb., mainly *Angelica arguta* Nutt. near mountains, no native records for prairies
P. zelicaon (western United States): wide variety of umb., esp. *Angelica* (eg. Emmel and Shields, 1979); rut. in some areas (esp. introduced *Citrus* in southern California)

P. polyxenes X *machaon* (central Manitoba): umb., mainly *Zizia*, also cultivated umb.

P. p. asterius (southern Manitoba): umb., mainly cultivated species, also on *Zizia*
P. p. asterius (western United States and Canada): wide variety of umb. (eg. Berenbaum, 1981), including all species fed on by *P. joanae*; occasionally on rut.
P. p. coloro: rut., esp. *Thamnosa montana* Torr. & Frem. (Ferris and Emmel, 1982)
P. p. polyxenes, *stabilis & americus*: variety of umb., esp. weedy species (eg. Blau, 1980; Brown, 1953; Riley, 1975)

P. joanae: umb.- *Taenidia integerima* L., *Thaspium barbinode* (Michx.), *Zizia aurea* L.(Koch) (Opler and Krizek, 1984)
P. brevicauda: umb., esp. *Ligusticum scoticum* L. (Ferguson, 1954; Jackson, 1982)
P. indra: variety of dryland umb., esp. *Lomatium* species (Emmel, 1975)

Figures 35 to 36. Locations of larvae collected on composites.

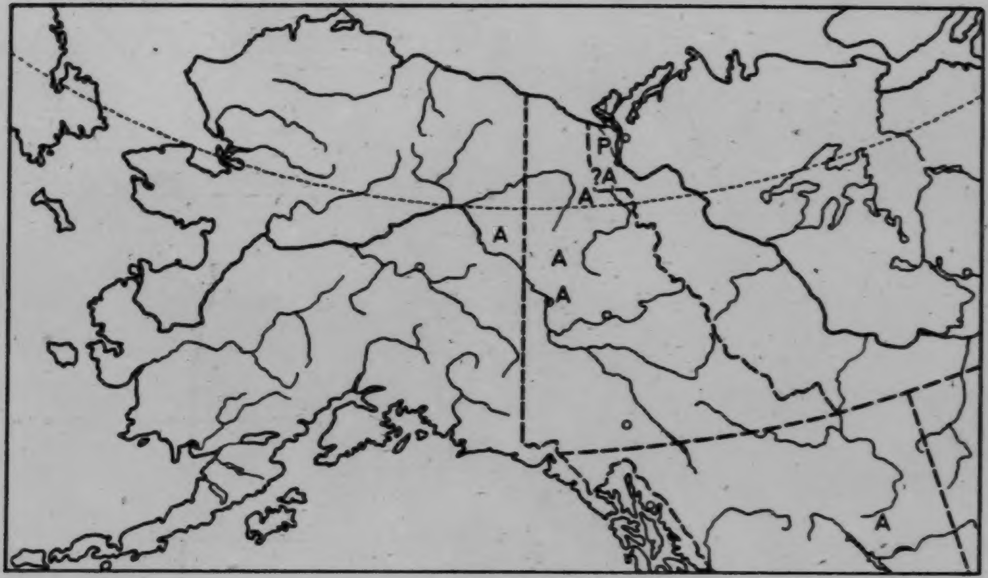
A = *Artemisia arctica* Less.

dots= *Artemisia dracunculus* L.

P = *Petasites palmatus* (Ait.)Gray

Figure 35. *P. machaon* larval records - Alaska and Yukon.

Figure 36. *P. machaon* larval records - Western Canada.



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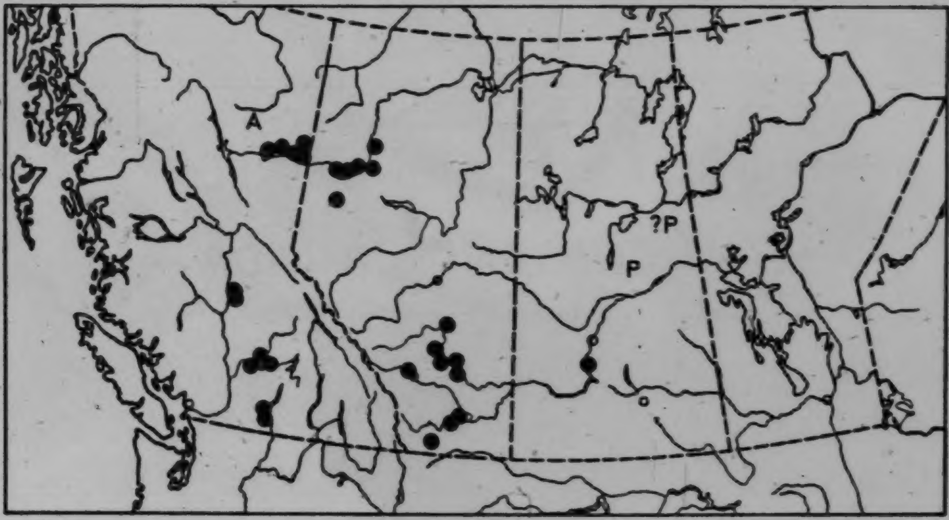

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Figures 37 to 38. Locations of larvae collected on umbellifers.

Figure 37. Larvae collected on plants of *Heracleum lanatum* Michx..

Figure 38. Larvae collected on other umbellifers.

Aa = *Angelica arguta* Nutt.

Ad = *Angelica dawsoni* S.Wats.

Ag = *Angelica genuflexa* Nutt.

Al = *Angelica lucida* L.

Co = *Cicuta occidentalis* Greene

Ld = *Lomatium dissectum* (Nutt.)Mathias & Constance

Ln = *Lomatium nudicale* (Pursh) Coult. & Rose

Lt = *Lomatium triternatum* (Pursh) Coult. & Rose

Oc = *Osmorhiza chilensis* Hook. & Arn.

Os = *Oenanthe sarmentosa* Presl.

S = *Sium suave* Walt.

Z = *Zizia aptera* (A.Gray)Fern

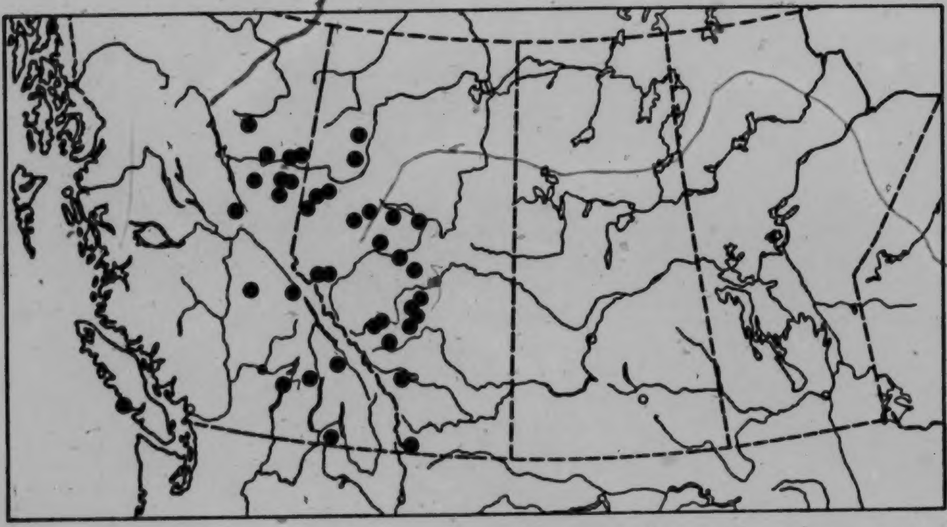
gc = garden carrot (*Daucus carota*) L.

gd = garden dill (*Anethum graveolens*) L.

ge = garden celery (*Apium graveoens*) L.

gn = garden parsnip (*Pastinaca sativa*) L.

gp = garden parsley (*Petroselinum crispum*) (Mill.)Mansf.



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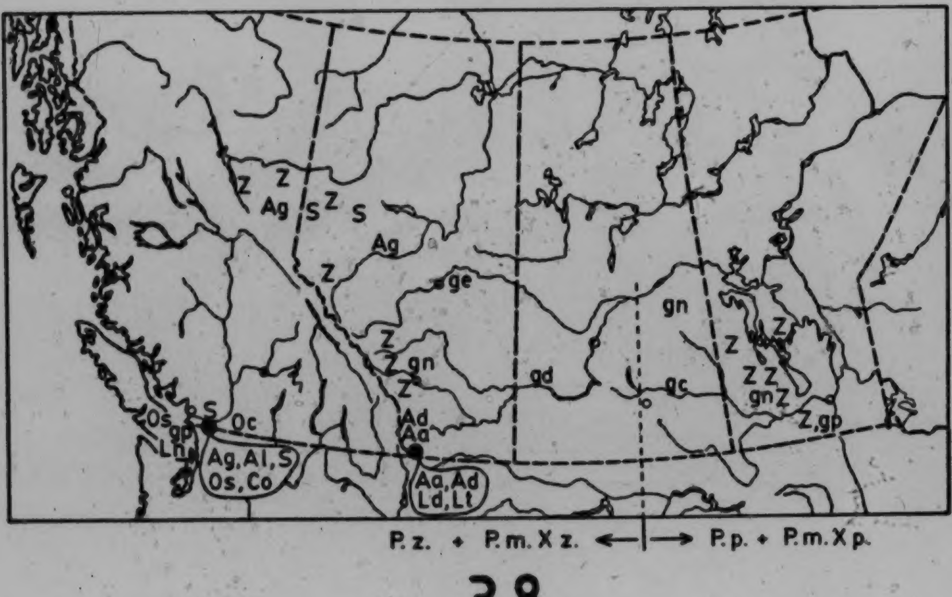
Z
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ZZ
gnZ
gc
Z,gp
Os
S
Oc
gp
Ln
Ag,Al,S
Os,Co
Ad
Aa
Aa,Ad
Ld,Lt
P.z. + P.m.Xz. ← | → P.p. + P.m.Xp.

38

A few larvae of *P. m. aliaska* may feed on umbellifers in nature, but no definite observations have as yet been made. Kimmich (1979), reported a female investigating plants of *Osmorhiza longistylis* (Torr.)DC at Stewart Crossing, Yukon Territory. He obtained oviposition on this and other species of umbellifers when the female was confined to these plants, and reared larvae to maturity on the plants. Kimmich (*in litt.* 1982) has also transferred small larvae of *P. m. aliaska* (which started feeding on *Artemisia arctica*), to *Heracleum lanatum* plants, and reared most of them through to maturity. As well, I have collected larvae of the *P. machaon* group on *H. lanatum* plants below Pink Mt., British Columbia. However, all died before emerging, and the larvae may not have been *P. machaon*, since *P. zelicaon* is found at Pink Mt. as well.

A single record of a wild collected larva is known for *P. m. hudsonianus* (Table 20). This is from northern Saskatchewan, where G. Anweiler (*in litt.* 1981) found a freshly molted fifth instar larva. Anweiler photographed the larva resting on the upperside of the leaf, with the fourth instar skin behind it, and feeding signs on the far side of the leaf. The plant species was *Petasites palmatus* (Compositae), a different variety of the same species on which Bryant (Leussler and Bryant, 1935), found *P. m. aliaska* larvae at Aklavik. Anweiler also observed oviposition by a female *P. m. hudsonianus*, which was reported by Hooper (1973) as being on black snakeroot

Sanicula marilandica L. (Umbelliferae). Hooper's report was based on Anweiler's verbal description of the plant, and could just as well refer to *Petasites palmatus*.

Many larvae of the *P. machaon* group have been found on plants of *Zizia aptera* (Umbelliferae) in central Manitoba. Though most of these develop into black morph adults (*P. p. asterius* or *P. polyxenes X machaon* hybrids), about 2% of them produce yellow adults similar to *P. m. hudsonianus* (*in litt.*, J. Troubridge). However, they all differ from typical *P. m. hudsonianus* in that they show a basally darkened, *avinoffi*-like wing pattern that suggests they are hybrids with *P. polyxenes*. Thus *P. m. husonianus* probably has a different larval foodplant from both *P. p. asterius* and hybrid swarms in areas where these come in contact. I have also reared adults very similar to *P. m. hudsonianus* from *P. zelicaon* X *machaon* hybrid populations at several localities on the east slope of the Rockies in Alberta. The foodplants included *Z. aptera* at Bragg Creek, and *H. lanatum* at Buck Lake and Nordegg.

Although the southern subspecies of *P. machaon* have previously been considered to be specifically distinct from *P. m. aliaska* and *P. m. hudsonianus*, it is clear that the differences in larval foodplant between these taxa are relatively small. Larvae of *P. m. pikei*, *P. m. oregonius*, *P. m. dodi*, and *P. m. bairdii* are all restricted to a single species of Compositae, *Artemisia dracunculus* (Table 11 and 20). Many larvae of *P. machaon* collected on *A. dracunculus* feed on umbellifers if they are transferred to them (Edwards, 1893, 1898; Emmel and Emmel, 1963; J. Troubridge, *in litt.* 1981; personal observation, 1982; but contrast Newcomer, 1964). However, mortality of these larvae is high on most umbellifer species. Larvae of *P. zelicaon* and *P. polyxenes*, for their part, refuse to feed on *A. dracunculus*.

P. zelicaon larvae feed on rutaceous plants as well as on a wide variety of umbellifers in the United States, and *Angelica* species seem to be especially favored (eg. Emmel and Shields, 1980). In contrast, *P. indra* larvae are found on narrower range of umbellifers, particularly *Lomatium* species (Emmel, 1975). Although largely separated by habitat, some *P. zelicaon* larvae feed on the same species of foodplants as those used by *P. indra* larvae.

In California, *P. zelicaon* larvae feed frequently on the introduced weedy umbellifer, *Foeniculum vulgare* Mill., and in some localities feed on *Citrus* (Rutaceae) orchards (Shapiro and Masuda, 1980). The foodplant shift to introduced umbelliferous and rutaceous plants has allowed *P. zelicaon* to produce several broods a year on these hostplants, rather than the single brood that is normally possible on native umbellifers (Emmel and Shields, 1980; Sims, 1980). Remington (1968) considered larval foodplant preferences as evidence for the specific distinctness of his *P. gothica*. However, the foodplant preferences he listed have been disputed by Emmel and Shields (1980), and I have confirmed their findings (Table 20).

In western Canada, only umbelliferous foodplants are known for larvae of *P. zelicaon* (Table 20, Figure 37 and 38). *Heracleum* plants are used commonly, though *Angelica* plants tend to be used mose frequently at localities where these plants are more numerous. Although plants of *Artemisia arctica* and *Heracleum lanatum* grow together near treeline at many sites in the Peace River region, I have seen no evidence to indicate that this leads to significant amounts of hybridization between *P. zelicaon* and *P. m. aliaska*.

Larvae of *P. zelicaon* X *machaon* populations in central Alberta also feed on umbellifers. At Bragg Creek, these populations show some segregation from *P. zelicaon* populations to the west and south, and the larvae feed mainly on plants of *Zizia*. In the northern part of central Alberta, the hybrid populations merge into typical *P. zelicaon*, and the larvae feed on *Heracleum* plants, a more common foodplant of *P. zelicaon*.

I have obtained black morph adults from two species of Umbelliferae. One specimen was obtained together with typical *P. zelicaon* on *Angelica arguta* at Waterton Park, Alberta. The other specimens were on *Zizia*, and were part of the hybrid population at Bragg Creek, Alberta. In both groups the black and yellow morph specimens were produced in similar proportions to those of wild collected adults. Hooper (1973) also reported both black and yellow morphs being produced from the same umbelliferous foodplant: garden dill (*Anethum graveolens*) at Eston, Saskatchewan. As well, I have reared one black morph adult from larvae of *P. m. dodi*, collected on *Artemisia dracunculus* at Taber, Alberta. These observations support the electrophoretic evidence, which indicates that the black adult morph is an integrated part of several taxonomically different *P. machaon* group populations in western Canada.

Larvae of *P. p. asterius* are found on a broad range of Umbelliferae and even a few rutaceous species (Berenbaum, 1981). Many of these are either introduced or common in cultivated areas, and so the fact that *P. p. asterius* is a common butterfly in much of eastern North America may be a recent phenomenon, aided by human agricultural patterns in the last two hundred years or so (Feeny *et al*, 1985). The pattern of dependence on weedy or cultivated foodplants seems to extend within the range of *P. polyxenes* at least to Costa Rica (Blau, 1980). Most larvae of *P. p. asterius* feed on foodplants different from those of *P. brevicauda* and *P. joanae* in areas where the two species contact each other (McDunnough, 1939b; Ferguson, 1954; Heitzman, 1973). However, *P. p. asterius* may occasionally be found on the same species which support *P. joanae* and *P. brevicauda*, and so these ecological distinctions between the two species are not major (Berenbaum, 1978).

Not all populations of *P. polyxenes* are dependent on umbellifers for larval foodplants, since *P. p. coloro* larvae feed mainly on plants of *Thamnosa* species (Rutaceae) in the desert areas of the southwestern United States. In this region *P. polyxenes* is in part sympatric with *P. m. bairdii* (larvae of which feed on *Artemisia dracunculus*), and *P. indra* (larvae of which feed on umbellifers). Emmel and Emmel (1969) described a population expansion of *P. indra* and *P. p. coloro* during which some larvae of either species had not only consumed their own foodplant but had also moved to a plant of the species normally used by the other butterfly species. Some of the larvae found on the wrong foodplant produced viable adults, which suggests some form of foodplant exclusion under normal conditions.

As with *P. zelicaon*, the larvae of *P. p. asterius* feed only on umbellifers in western Canada. However, the larvae of *P. p. asterius* frequently use introduced and cultivated foodplant species, while this is more infrequent for *P. zelicaon* larvae. I have been able to examine adult specimens reared from two introduced foodplant species in Manitoba and Saskatchewan. These include a series of four specimens reared on *Pastinaca* at Somme, Saskatchewan, and another of five specimens reared on *Petroselinum* at Culross, Manitoba (Table 20). Both of these series contain specimens ranging from typical *P. p. asterius* to at least one which was more typical of the *P. polyxenes X machaon* hybrid populations which are common in forested areas.

In the zone of interaction between *P. p. asterius* and *P. m. hudsonianus* in central Manitoba, the native umbellifer, *Zizia aptera*, is the primary larval foodplant (Table 20, Figure 38). *Z. aptera* plants are more characteristic of open meadows than forests, and so are not a major factor in the partial habitat separation between *P. polyxenes* and *P. polyxenes X machaon* hybrid populations. Other references to native umbelliferous foodplants for hybrid populations include "meadow parsnip" (*Zizia*[?] - Hooper, 1973), and cow parsnip (probably *H. lanatum* - Tyler, 1975), which I have not been able to confirm.

5.1.4 Parasites in western Canada

A number of parasites were obtained in the course of the collection and rearing of immatures of the *Papilio machaon* group from western Canada. All were Hymenoptera or Diptera (Table 13).

No parasites except for *Trogus* species parasitized more than 5% of the *P. machaon* larvae in a population. *Trogus* parasites exceeded this level only in the Peace River region, where more *Trogus* adults than *Papilio* adults were obtained from many samples of reared *Papilio* pupae. The frequency of parasitism of *Papilio* immatures is also variable outside western Canada. For example, parasites of *P. polyxenes* are rare in Costa Rica (Blau, 1980:323), but more common in New York (Blau, 1981:79; Feeny *et al*, 1985:177).

Parasites were found on several immature stages of hosts of the *P. machaon* group. Mature larvae of *Cotesia* emerged from third instar *Papilio* larvae before spinning a coccoon nearby, in which to pupate. There was only one

Table 14. Parasite records.

Entries arranged by parasite species, followed by host species. The number of adult parasites obtained are indicated behind each entry. Except for the *Trogus lapidator* on *P. polyxenes* X *machaon* (collected by P. Klassen) and the *Cotesia* (collected by H. Kimmich), all adult specimens were obtained by F.A.H. Sperling. All records are from western Canada, except for parasites on *P. p. asterius*, which were received in specimens reared in southern Ontario.

1. **Braconidae** - determined by D.J.M. Williams, 1983

Cotesia sp. nr. *nemoriae* Ashmead
    P. machaon oregonius (3)

2. **Ichneumonidae** - determined by R.T. Mitchell, 1983

Trogus lapidator panzeri Carlson: *P. m. aliaska* (8),
    P. m. pikei (21), *P. m. dodi* (5), *P. zelicaon* (3),
    P. zelicaon X machaon (6), *P. polyxenes X machaon* (2),
Trogus lapidator brevicaudae Heinrich: *P. m. pikei* (3)
Trogus pennator var. *fulvipes* Cresson:
    P. m. pikei (7), *P. zelicaon* (2),
Trogus pennator (Fabricius): *P. p. asterius* (2)

3. **Pteromalidae** - determined by G.A.P. Gibson, 1984

Pteromalus sp., possibly *P. cassotis* or *P. vanessae*
    P. m. pikei (numerous parasites from one pupa)

4. **Tachinidae** - determined by J.E. O'Hara, 1981 to 1983

Madremyia sp.: *P. m. pikei* (1)

Compsilura consinnata (Meigen): *P. p. asterius* (1)

Buquetia obscura (Coquillett):
    P. m. oregonius (3), *P. zelicaon* (2)

parasite per host individual. Larvae of *Buquetia obscura* emerged from large fifth instar host larvae, with two to four parasites per host. The single *Madremyia* larva which I have reared was visible in the mature host larva as a large brown bruise, but did not emerge from the host until three weeks after it had pupated. Only one *Compsilura* larva emerged from the host pupa as well, but did not do so until the host had already deposited pigment in the wings and was about to emerge. The *Pteromalus* wasps emerged about one month after the host had pupated, with several dozen adults emerging from a single host pupa. This record was supplied by E.M. Pike, who was rearing the host at Fairview, about 16 km from its normal range, and also observed the female *Pteromalus* laying eggs on the freshly pupated host.

Trogus females probably lay eggs only on host larvae in the fourth or fifth instar, judging from the absence of these parasites in individuals collected as early larval instars. As well, parasitism of *P. machaon* by *Trogus* seemed to be more common in host larvae which were collected after most larvae in a population had already pupated. *Trogus* wasps generally began to emerge about a week after adult *Papilio* began to emerge from the same population. A single *Trogus* wasp emerged from each host individual, from a large hole in the side of the pupa.

None of the parasite species appeared to distinguish among host species of the *P. machaon* group. *Trogus* species parasitized a variety of species of *Papilio*, and are also known from the papilionid genus *Graphium* (Mitchell, 1979). My own records confirm that *Trogus* species do not appear to select any particular species of the *P. machaon* group to parasitize.

Although the braconid species in Table 14 only has *P. m. oregonius* listed as a host, this same undescribed species has also been found on *P. zelicaon* in California (D.J.M. Williams, pers. comm.). The tachinid species probably have the widest host range of the parasites listed. Both *Compsilura* and *Madremyia* flies parasitize a wide range of lepidopterous families, as well as beetles of the family Curculionidae (Arnaud, 1978). *Buquetia obscura* parasitizes *Danaus plexippus* (L.) (Danaidae), as well as *Papilio polyxenes* (Arnaud, 1978).

Although they do not show species-specific host-parasite relationships, both the *Papilio machaon* group and the genus *Trogus* appear to be undergoing extensive hybridization in western Canada. All nine adults of *Trogus pennator* var. *fulvipes* obtained in Alberta and northern British Columbia showed a degree of wing infuscation intermediate between the state typical of *T. lapidator* and the state in *T. pennator* var. *fulvipes* in the eastern part of its range (R.T. Mitchell, *pers. comm.*). As well, two of the nine had black hind tarsi which resemble the state normally found only in *T. lapidator panzeri*.

Of the 46 specimens of *T. lapidator* obtained from Alberta and northern British Columbia, 14 (30%) had character states intermediate between *T. pennator* and *T. lapidator*. R.T. Mitchell identified these specimens and commented (*in litt.* 1983) that "Canada seems to be a real melting pot of *Trogus*". Even if the two species of *Trogus* parasitizing the *Papilio machaon* group in western Canada turn out to be different forms of a single polymorphic species, it is interesting to note that systematic relationships among *Trogus* species show parallels with relationships within the *P. machaon* group. These similarities are probably due to a common biogeographic history, to be discussed in the chapter on geographic history of the *P. machaon* group.

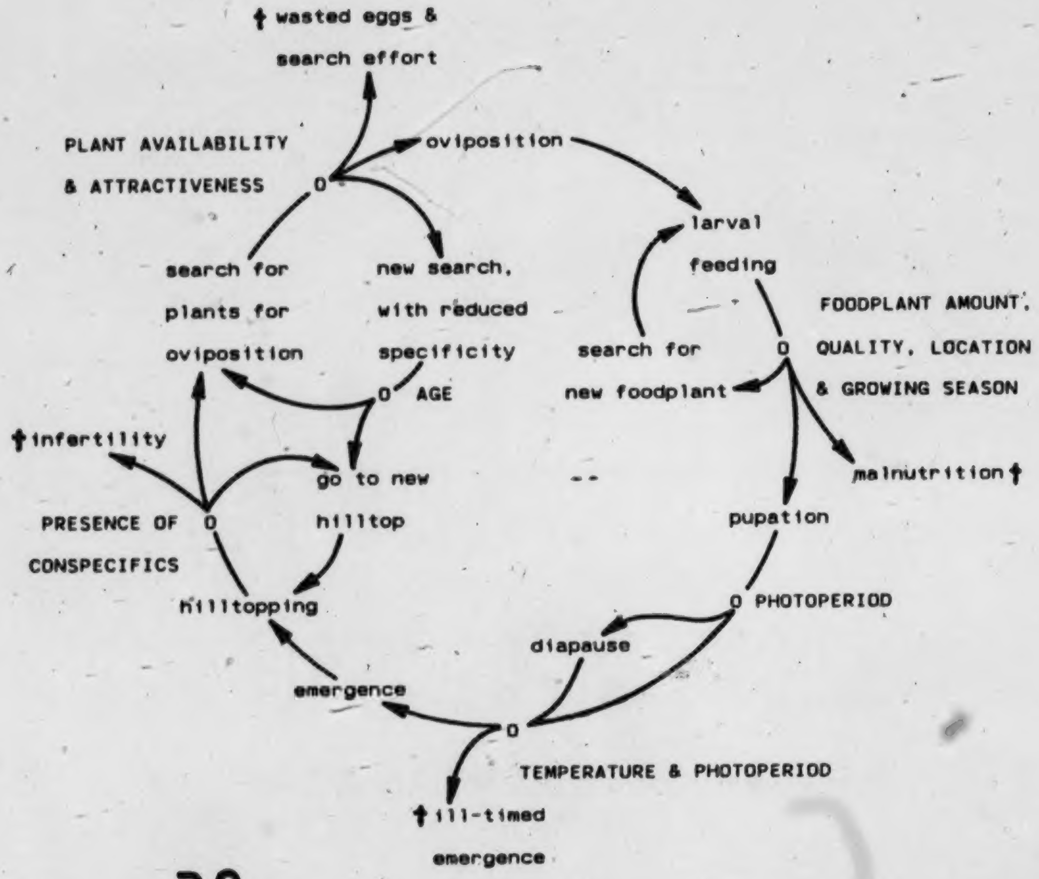
5.2 Local Adaptations

The process of differentiation into taxonomically distinct populations involves many mechanisms similar to those which are important to the adaptation of demes to local conditions. Local adaptation occurs in different ways throughout the life cycle of populations (represented in Figure 39). Such mechanisms of adaptation predominantly involve foodplant quality, availability and seasonality, genetic variation among *P. machaon* group populations and, the presence of related *P. machaon* group species.

5.2.1 Foodplant suitability and availability

The availablity of different foodplants for use by *P. machaon* group larvae in different geographic areas of

Figure 39. Major sites of adaptation within life cycle. Factors influencing local selection are indicated in capital letters, and "O" refers to site of selection. Causes of loss of fitness are indicated by "†". Predators and/or parasites, and weather factors, such as rain, directly reduce fitness in all parts of life cycle, and are not specifically listed.


† wasted eggs & search effort
PLANT AVAILABILITY & ATTRACTIVENESS
O
oviposition
larval feeding
search for plants for oviposition
new search, with reduced specificity
O AGE
search for new foodplant
O
FOODPLANT AMOUNT, QUALITY, LOCATION & GROWING SEASON
†infertility
go to new hilltop
malnutrition †
PRESENCE OF CONSPECIFICS
O
pupation
hilltopping
O PHOTOPERIOD
diapause
emergence
O
TEMPERATURE & PHOTOPERIOD
† ill-timed emergence

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western Canada is probably influenced by several major factors. One of these is the relative suitability of potential hostplants. For example, plants of *Angelica* species, when available, appear to be preferred over most other native umbellifers for oviposition by *P. zelicaon* females in the wild. This preference is especially clear at Waterton, in southwestern Alberta (Table 20). Emmel and Shields (1980) also found that *Angelica* species were especially commonly used by *P. zelicaon* in the southwestern U.S., while Wiklund (1974a) found the same for *P. machaon* in Sweden.

This trend may be partly related to the nutritional suitability of leaves. Erickson (1975) and Scriber and Feeny (1979) found that *P. polyxenes* and lab-reared *P. polyxenes X zelicaon* hybrids had very good to moderate growth rates on *Angelica* species from New York, while Wiklund (1975) found that *P. machaon* larvae had low to moderate mortality on *Angelica* species in Sweden. Wiklund (1973, 1974b, 1975) also showed that the hierarchy of larval foodplant suitability was related to ovipositional preferences by female *P. machaon*, and was not influenced by the plant on which the female had fed during the larval stage. These studies indicate that *Angelica* species generally are good hostplants for larvae of the *P. machaon* group, though there is some variation in suitability between *Angelica* species.

The other umbellifer species used by larvae of the *P. machaon* group in western Canada are more varied in the degree to which they are suitable for larval growth. *Zizia aptera* and *Sium suave* give good growth for larvae of *P. polyxenes* (Erickson, 1975; Scriber and Feeney, 1979), while *Heracleum lanatum* is a relatively poor hostplant (Erickson, 1975). Since *H. lanatum* is a major foodplant of *P. zelicaon* in western Canada, the *P. zelicaon* populations have probably developed better physiological adaptations to this foodplant than has *P. polyxenes*. Nonetheless, there is evidence that the preferred foodplants of *P. machaon* group species tend to share a number of biochemical constituents, such as furanocoumarins (Berenbaum, 1981). The use of a limited number of rutaceous and composite species is no accident as well, since these are biochemically rather similar to umbellifers (Dethier, 1941).

It is reasonable to expect that plant size also influences the suitability of various umbellifers as hostplants. Small plants such as *Zizia aptera* may not have enough tissue to feed a larva to full maturity (personal observation). The leaf tissue may be quite suitable for growth, but if larvae have to search out a new plant before they are full grown (as in *Battus philenor* [L.] on *Aristolochia*, Rauscher 1980), then mortality may be unusually high. Such a situation should cause selection against oviposition preferences for *Zizia* by females.

On the other hand, large-leaved plants such as *Heracleum* and *Angelica* may provide more than enough plant tissue, but expose larvae to more predation. I have found larvae to be much easier to locate on large-leaved plants than small or narrow-leaved plants. The importance of visual predators was shown by Blau (1980, 1981b), who reported that large predators (which could not penetrate a 1.3 cm mesh) were the most important mortality factor for *P. p. stabilis*. However, Järvi *et al* (1981) showed that *P. machaon* larvae are distasteful and survived attacks by even naive individuals of the great tit *Parus major*.

Leaf shape may also affect the efficiency of hostplant searches by females. Rauscher (1978, 1980) found that *Battus philenor* females could change their search image during their lifetime, but tended to find only one of two *Aristolochia* leaf types in any one time period. Umbellifers vary considerably in leaf shape and so a visual search image may be less important to females of the *P. machaon* group than to *B. philenor*. At Waterton, larvae were found on leaves which varied in shape from the palmate leaves of *Heracleum* to the long and very narrow leaves of *Lomatium triternatum*. Nonetheless, major differences in leaf shape could influence females to not lay eggs on plants which have a strikingly different leaf shape from their normal hostplant. Such a situation may exist at Pink Mountain, British Columbia, where most *P. m. aliaska* females oviposit on plants of *Artemisia arctica*, which have dissected leaves somewhat like domestic carrots, and not on *Heracleum lanatum*, which is a much larger plant with large palmate leaves.

In addition to the suitability of foodplants for larval feeding, the geographic availability of different foodplant species may be a major influence on the pattern of use of larval foodplants. The geographic distribution of hostplants, combined with a hierarchy of nutritional suitability, explains some of the shifts in local foodplant use in western Canada. For example, demes of *P. zelicaon* depend mainly on *Heracleum* in northern Alberta, where *Angelica* plants are uncommon, but depend on *Angelica* in southern Alberta, at Waterton, despite that *Heracleum* is common at Waterton. Both *A. arguta* and *A. dawsoni*, as well as *Lomatium triternatum* and *L. dissectum*, are restricted to the southwest corner of Alberta (Moss and Packer, 1983), and so it is only in that area that any one of these species could become a major foodplant. On the other hand, the absence of *P. machaon* group species in the north eastern part of Alberta is only dubiously due to a paucity of foodplants, since I have found both *Zizia* and *Heracleum* plants to be common there.

5.2.2 Diapause and voltinism

Diapause and voltinism are important components of the adaptations of populations to local conditions. Since individuals can maximize their reproductive fitness by foregoing diapause when another generation is still possible within the growing season, there is selection against genomic combinations which cause an individual to enter diapause prematurely. However, diapause in temperate regions is posssible only in the pupal stage, and failure to reach pupation results in death of the individual (though it is possible that some fifth instar larvae diapause in warm, dry climates - Wiltshire, 1958). This provides a strong opposing selective pressure for pupae not to emerge if there is not enough growing season left to produce another generation. The presence of such selection accounts for the existance of mechanisms allowing *P. machaon* group species to adapt relatively quickly to local conditions.

The mechanisms which allow *P. machaon* group taxa to adapt to local conditions involve genetically determined responses to environmental cues for diapause induction and termination. In temperate regions, pupal diapause is induced if late instar larvae are reared under short daylength conditions. Since populations at northern latitudes experience longer days but a shorter growing season, these populations undergo diapause in response to relatively longer photoperiods than do southern populations. The genetic basis of such differences in diapause induction has been demonstrated several times (Oliver, 1969; Sims, 1980 & 1983; and Blau, 1981a & 1981c).

The termination of pupal diapause is usually induced by exposure to warm conditions after an extended period of cool temperature. When diapausing pupae are refrigerated for longer periods of time, emergence of adults occurs sooner and in a more synchronized pattern (Shimada, 1976).

Termination of pupal diapause also depends on sufficient temperatures for physiological development, as well as on daylength (as in *P. m. pikei*).

The phenological characteristics of larval foodplants are major influences on these characteristics in *P. machaon* group populations. Blau (1981c) showed that the timing of *P. polyxenes* broods is related to the temporal distribution of the hostplants, and escape from foodplant patches of decreasing quality is accomplished by diapause in New York populations and dispersal of females in Costa Rica. As well, the evolution of multivoltinism in most regions where *P. machaon* group populations have switched to introduced foodplants is almost certainly a response to the availability of these foodplants over a much greater proportion of the year than native foodplants.

Foodplant phenology, together with accumulated degree days, can account for the unusually late flight period of *P. m. pikei* in the Peace River region, compared to that of *P. m. oregonius* and *P. m. dodi* adults in southern British Columbia and Alberta. This difference in flight time is especially noticable when one considers that *P. m. dodi* adults are out early in the flight periods of such species as *Oeneis uhleri* Reakirt and *Papilio glaucus* in southern Alberta, but *P. m. pikei* adults do not fly until after the main flight of these species in the Peace River region. Since the region is a considerable distance to the north of the ranges of *P. m. dodi* and *P. m. oregonius*, the growing season is not long enough for the Peace River populations to produce even a partial second brood (Figure 34). As well, it is possible that *P. m. pikei* may have fixed genes for univoltinism, since it has probably recently been derived from the univoltine alpine *P. m. aliaska*. Without selection pressure to produce the first brood larvae as quickly as possible to allow time for second brood larvae to develop, the first brood larvae are free to develop later in the season, when the foodplant has larger amounts of lush foliage, compared to earlier in the spring. Since most umbellifers have become senescent by late summer in this area, the option to delay adult emergence is not available to the univoltine *P. zelicaon* populations in the region.

Environmental stability may also be a strong influence on phenology and diapause behavior in *P. machaon* group species. If habitat suitability is relatively unpredictable, then a variety of risk spreading mechanisms can be expected (den Boer, 1968; Stearns, 1976). Extended pupal diapause is an important example of such a mechanism in the *P. machaon* group, especially in arid habitats. There are two components to extended diapause. One component is an emergence in which adults from a single cohort emerge at low frequencies over an entire growing season, and in doing so increase the chances that at least some of them will be out during a period of good larval foodplant abundance. The other component is a particularly long diapause, in which a proportion of the population remains in diapause through one or more growing seasons, spreading the risk of unpredictable mortality over more than one year. Since arid habitats are especially susceptible to irregular rains, the dryland *P. machaon* group populations should be more likely to show extended emergence. This certainly holds true for pupae which have emerged under laboratory conditions. The populations showing the most extended emergence, both within an emergence period and between such periods, were the dryland *P. machaon* from southern Alberta and the Peace River region.

An additional advantage of extended pupal diapause is that it may allow populations which survive a bad growing season to be relatively free of parasites. For example, *P. m. pikei* pupae frequently went through more than one cool cycle before emerging, but only one *Trogus* individual emerged after two cycles of refrigeration. Since the only populations of the *P. machaon* group which had heavy parasitism rates belonged to *P. m. pikei*, such a mechanism may be important to the avoidance of parasites by these populations.

Not all dryland *P. machaon* populations show extended emergence within a growing season or over more than one season. For example, there is major variation within *P. m. dodi* with respect to the amount of time it takes for adults to emerge from overwintered pupae under laboratory conditions. There appear to be two types of populations. One type has an emergence pattern much like *P. m. oregonius* from southern British Columbia, with synchronous emergence a few weeks after removal from refrigeration and no adults coming from pupae in extended diapause. This emergence pattern is found in pupae from along the Oldman River and its tributaries in southern Alberta (n=58 laboratory emergences), as well as at Outlook in Saskatchewan. The second type of emergence pattern is characterized by very extended, asynchronous emergence within a season, and a significant proportion of individuals which remain in pupal diapause throughout at least one growing season. This pattern is seen in the *P. m. dodi* populations along the Red Deer River, in the northern half of the southern Alberta grasslands (n=39 laboratory emergences). The adaptive significance of this variation may be related to the high frequency of late spring frosts which occur in the area between Red Deer and Drumheller (Canadian Climate Normals, 1951-1980. [1982d]), and which may be particularly damaging to pupae during the vulnerable period just before emergence.

5.2.3 Genetic variation

Variation in genetic composition among demes of species of the *P. machaon* group is also a major factor in local adaptation, by determining what plants are available and suitable as larval food. Gene pools will themselves depend on the evolutionary history of a population, including factors such as recent selection, introgression, mutation or random drift. Scriber and Feeny (1979) pointed out that *P.*

zelicaon larvae from California had relatively poor growth on plants such as *Pastinaca*, which are major foodplants of *P. polyxenes* in the northeastern states. Oliver (1969), Sims (1980) and Blau (1981a and 1981c) showed significant variation within *P. polyxenes* and *P. zelicaon* with respect to traits related to hostplants, such as diapause induction and egg production.

Adaptive divergence between different populations within species is probably an important factor in foodplant use in *P. machaon* group species in western Canada. Though plants of *Heracleum lanatum* are generally less nutritionally suitable for development by *P. zelicaon* than those of *Angelica arguta*, it is conceivable that larvae from central Alberta which have had to adapt to *Heracleum* would do less well on *Angelica* than larvae from Waterton. Correspondingly, it may be that there is enough population variation within plant species so that the process of local adaptation takes place even for specialist populations. For example, it is my impression (though I have not rigorously collected data) that *P. machaon* larvae from *Artemisia dracunculus* in southern Alberta, southern British Columbia and along the Peace River grow better on plants from their own area than from other areas.

The successive accumulation by a population of genetic adaptations may give it an advantage in being able to switch back to ancestral foodplants. Foodplant reversals to rutaceous plants are obvious examples, and may involve cultivated species, such as *Ruta* in Bagdad (Wiltshire, 1958), or native species, such as *Thamnosa* in Arizona (Ferris and Emmel, 1982). The phenomenon undoubtedly occurs within umbelliferous hostplants as well, though it is would be more difficult to detect. Since composite-feeding habits evolved relatively recently, fewer opportunities for reversals to umbellifers may have occurred. However, the potential certainly exists, and it would be interesting to see if these *P. machaon* larvae are able to go back two evolutionary steps and accept rutaceous species as larval foodplants.

Shifts to introduced and cultivated foodplants also give some indication of the speed with which local genetic adaptation may occur. Examples from North America are especially good indicators, since the continent has only relatively recently been subjected to widespread agriculture. Adaptation in phenology and foodplant use has occurred in central California, where *P. zelicaon* is now multivoltine on introduced foodplants but was derived within the last 150 years from populations which were univoltine on native foodplants (Emmel and Shields, 1979; Shapiro and Masuda, 1980; Sims 1980 & 1983). The widespread use by *P. polyxenes* of cultivated umbellifers, and the opening up of large forested areas in eastern North America may have allowed *P. polyxenes* to expand its range within a similar time frame. It is also conceivable that the occurrence of *P. polyxenes* in South and Central America may have been aided by the growth of weedy umbellifers in areas of primitive agriculture in the last few thousand years.

5.2.4 Effects of interspecific interactions

Other than foodplant suitability and availability, combined with variations in genetic composition at the population level, interactions between species are a possible influence on local variation in larval foodplant choice. These interactions may occur in several different ways. I examine three separate explanations for why *P. machaon* group species may use different foodplants when they occur in sympatry.

One hypothesis is that competition occurs through the exclusion of the larvae of one species from the foodplant of another more successful species. Miller and Brown (1983) suggested that this may explain divergence in foodplant use within the *P. machaon* group. However, Ehrlich and Murphy (1983) stated that no such example of direct competition had yet been demonstrated in herbivorous insects.

Limitation of population size by a resource is a basic prerequisite that must be shown for competition studies. Here the resource is the foodplant, and larvae of one species must be able to preclude full use of the plant by larvae of another species. Blau (1980) indicated that in *P. polyxenes* in Costa Rica, large larvae may dislodge smaller larvae and eggs from their foodplants. This factor accounted for 8% of the total mortality in larvae of the second generation in one foodplant patch. In western Canada, I have on numerous occasions seen several incompletely grown larvae resting on the bare stems of their foodplants. Though on each of these plants the larvae might have been siblings from a single female, it is reasonable to suppose that instances occur in which the larvae would represent more than one species.

Even if the coexistence of the larvae of two species on a single plant does not result in direct dislodging or increased mortality due to having to find another foodplant before development is complete, the combined larval densities may be high enough to cause unusual mortality for both species. To my knowledge none of the parasites and predators on *P. machaon* group larvae are species specific, and high densities of larvae may even cause proportionately higher mortality due to these factors. The most noticeable example of this effect is mortality due to disease, which is frequently reported for crowded laboratory colonies. Although Blau (1980) did not find disease incidence to be significant in natural populations in Costa Rica, I have observed several examples of natural mortality due to disease. These almost always occurred in conjunction with relatively high population densities of larvae. The most extreme example occurred at Waterton in August of 1981, where I found three fourth-instar larvae dead on leaf tops, surrounded by the brown liquid which is characteristic of diseased lab cultures.

These observations indicate the potential for competitive interactions among larvae, but more work is needed before it can be shown that such interactions may be important enough to cause divergence in foodplant use. A good area in which to experimentally study interspecific interactions between larvae is southern California, where such factors may limit the range of *P. polyxenes*. Ferris and Emmel (1982) reported that females of *P. p. coloro*, whose larvae normally feed on wild rutaceous plants, sometimes oviposit on umbellifers at the edge of the species range in California, but larvae did not appear to be able to establish themselves on these plants where they were normally occupied by *P. zelicaon* larvae.

Divergence in foodplant use may occur through interactions between adults as well. In many areas, the larvae of two species may feed on different foodplants in a given area, but individuals may contact each other regularly as adults. In these areas some mechanism for species segregation in adults can be assumed. For example, Scott (1975) and Shapiro *et al* (1981) reported that *P. indra* adults fly just below the crests of hills, rarely mixing with the much more numerous *P. zelicaon* adults at the top. The congregation of males at topographic prominences, referred to as hilltopping (Shields, 1967), is a very pronounced trait throughout the *P. machaon* group and results in the mixing of species from a fairly large area. I have found *P. machaon* and *P. zelicaon* males hilltopping together at several localities, and though random mating does not seem to ensue, some hybrid individuals may be produced. Thus mate recognition in complete sympatry is not always perfect between species, and one would expect natural selection to also produce other mechanisms to reduce the loss of genes in such matings.

In the *P. machaon* group such mechanisms appear to commonly involve habitat selection, which results in species segregation in different habitats, and reduction in loss of viable adults to interspecific matings. Thus, in a sense, mate competition may lead to the occupation of different habitats by different species. Since different habitats may be occupied by species whose larvae feed on different foodplants, larvae might appear to do so because of competition when this may not actually have been the causal factor in the divergence in foodplant choice.

Habitat selection due to mate competition thus provides a second explanation for divergent foodplant use by two species in sympatry, though sympatry in such an area is defined rather broadly. It seems likely that *P. machaon* and *P. hospiton* maintain their integrity largely by this mechanism (Kettlewell, 1955). Another example is the *A. dracunculus*-feeding populations of *P. machaon dodi* in southern Alberta, adults of which generally hilltop on high riverbank edges, while *P. zelicaon* adults in the same area are found almost exclusively on wooded prairie hills.

A third explanation for divergent foodplant use is that it does not involve competition, but rather is the result of opportunistic random preadaptation for later coexistence in sympatry with another species. I have discussed several examples of geographic variation in foodplant use within a species, some of which have involved opportunistic reversals to the more ancestral rutaceous foodplants. *P. machaon*, however, has aquired a derived trait, in that some populations feed on composites. This evolutionary novelty may well have been acquired in isolation from other species of the *P. machaon* group. It is maintained at present in *P. m. aliaska* and *P. m. hudsonianus* in the absence of potential congeneric competitors, and may even be an important local adaptation in *P. machaon* in Afghanistan. Preadaptation in allopatry is a plausible explanation for the initial development of composite-feeding habits in *P. machaon*. However, these habits have since allowed *P. machaon* to occupy large regions in sympatry with *P. zelicaon* and *P. indra*, both of which continue to depend mainly on umbellifers. A possible scenario for development of such foodplant adaptation is outlined in the following chapter.

The diversity of mechanisms for local adaptation within the life cycle of *P. machaon* group individuals (Figure 39) illustrates the potential complexity of genetic interactions involved. A simple switch in larval foodplant may not only necessitate physiological adaptations for more efficient digestion, but also changes in oviposition behavior and pupal diapause, and may provide a mechanism for interspecific coexistence. Such considerations support the view that the process of local adaptation, much less speciation, involves a substantial reorganization of polygenic balances, with an irregular rather than strictly gradual evolutionary pattern over time.

6. EVOLUTIONARY HYPOTHESES

6.1 Origin and Early Differentiation of the *P. machaon* Group

The outgroup relationships of the *P. machaon* group are uncertain. Monroe (1961) was unable to resolve the affinities of the *P. machaon* group to other species groups in the genus *Papilio*. He only associated it with the *P. xuthus* group, and suggested that these two groups had affinities with the *P. demoleus* L. and *P. anactus* Macleay species groups. Ae (1979) presented data about interspecific hybridization which suggested that the *P. machaon* group was about as closely related to the *P. xuthus* group as it was to the *P. paris* L. group, which Monroe did not include in his reconstructed phylogeny. Ae also showed that the affinities of the *P. machaon* and the *P. demoleus* groups were probably still more distant. Hancock (1983) ranked the *P. machaon* group as a distinct genus with only primitive relationships to most of the remainder of the Papilionini. He also suggested that *P. alexanor* may represent a lineage predating a split between the *P. machaon* group and more than half of the species groups in the Papilionini.

I agree that *P. alexanor* must have diverged from the remainder of the *P. machaon* group much earlier than any of the other species in the group. For that reason, as well as the fact that its inclusion in the *P. machaon* group on the basis of larval characters is so strongly contradicted by the adult characters, I consider it with some caution in my discussion of the phylogeny of the *P. machaon* group.

Because relationships of the *P. machaon* group within the genus are uncertain, it is difficult to determine which character states within the group are plesiotypic. If the common-is-primitive method is applied to all the potential outgroups of the *P. machaon* group then *P. machaon* probably qualifies as the most plesiotypic species in the group. The application of such a procedure would eliminate most of the character states of the wing and body color pattern of *P. p. asterius* as likely primitive states.

Another method of polarizing character states has been applied by Seyer (1982) to the *P. machaon* group. He considered genetically dominant traits to have been more recently derived than traits which are more recessive. Since the allele for the black wing morph of *P. p. asterius* is dominant over the yellow allele, it was considered derived relative to the yellow morph. On this basis Seyer (1982) concluded that *P. zelicaon* was phylogenetically older than *P. machaon*, *P. hospiton* and *P. polyxenes*.

Despite the uncertainty involved in such an undertaking, I offer a tentative hypothesis on what the most recent common ancestor of the *P. machaon* group, excluding *P. alexanor*, may have looked like. My identification of primitive character states is mainly determined by the similarity of these states to states occurring frequently in different possible outgroups. On this basis, the ancestral species was probably very similar to present day *P. machaon*, though differing in several respects (Table 15). The differences from *P. machaon* in adult characters would include: 1) a more rounded hindwing pupil, 2) more black scales between the red and blue of the anal eyespot, 3) a less extensive suffusion of yellow scales on the wing surfaces, 4) more dark scales on the base of the hindwing, though not covering more than half of the hindwing disc, and 5) a shorter tooth row on the male genitalia. In these respects the ancestral species may have been more similar to either *P. hospiton* or *P. p. americus* (Table 15). The larvae would have had a banded color pattern and orange spots, and would have predominantly fed on umbellifers.

The ancestral species probably lived in the central Palearctic region, though it must have dispersed to North America very early in the development of the *P. machaon* group. This species certainly lived before the Pleistocene, considering the amount of differentiation within the group, though I doubt that the present species in the *P. machaon* group (excluding *P. alexanor*) began to diverge from each other much before the beginning of the Pleistocene (Figure 39 and 40).

Nei's (1972) genetic distance (D) can be used as a rough indicator of the time of divergence of two lineages. Thorpe (1982:153) used a D value of 1.0 to indicate a divergence time of 15-20 million years. When this ratio is applied to a value of 0.2 for interspecific comparisons within the *P. machaon* group (Table 6), then a divergence time of 4-5 million years is obtained for the three species now occurring in western Canada. For the subspecies within *P. machaon*, divergence times of 0.1 to 1.0 million years are indicated. Although these estimates are likely to be only roughly accurate, they nonetheless support the contention that the main lineages of the *P. machaon* group diverged before the Pleistocene, while most evolution within lineages took place during the Pleistocene.

The species which appeared during this time period probably gave rise to four major lineages in the *P. machaon* group. These lineages include what are now: 1),*P. machaon* and *P. hospiton*; 2), *P. zelicaon*; 3), *P. polyxenes*, *P. joanae* and *P. brevicauda*; and 4), *P. indra*.

The oldest of these four lineages is probably the one that gave rise to *P. machaon* (Figure 40 and 41). Both *P. hospiton* and *P. machaon* possess very few of the apotypic character states of the remaining lineages (Table 15). As well, it is more parsimonious to hypothesize that the *P. machaon* lineage evolved in Eurasia, and is not the product of a return dispersal from North America.

However, the common ancestor of the remaining lineages probably fragmented soon after colonizing North America. Both electrophoretic characters (Table 6) and hybridization in the laboratory (Ae, 1979) indicate that *P. machaon*, *P. zelicaon* and *P. polyxenes* are approximately equidistant from each other. Also, natural hybridization occurs between each of these three species pair combinations, as well as between

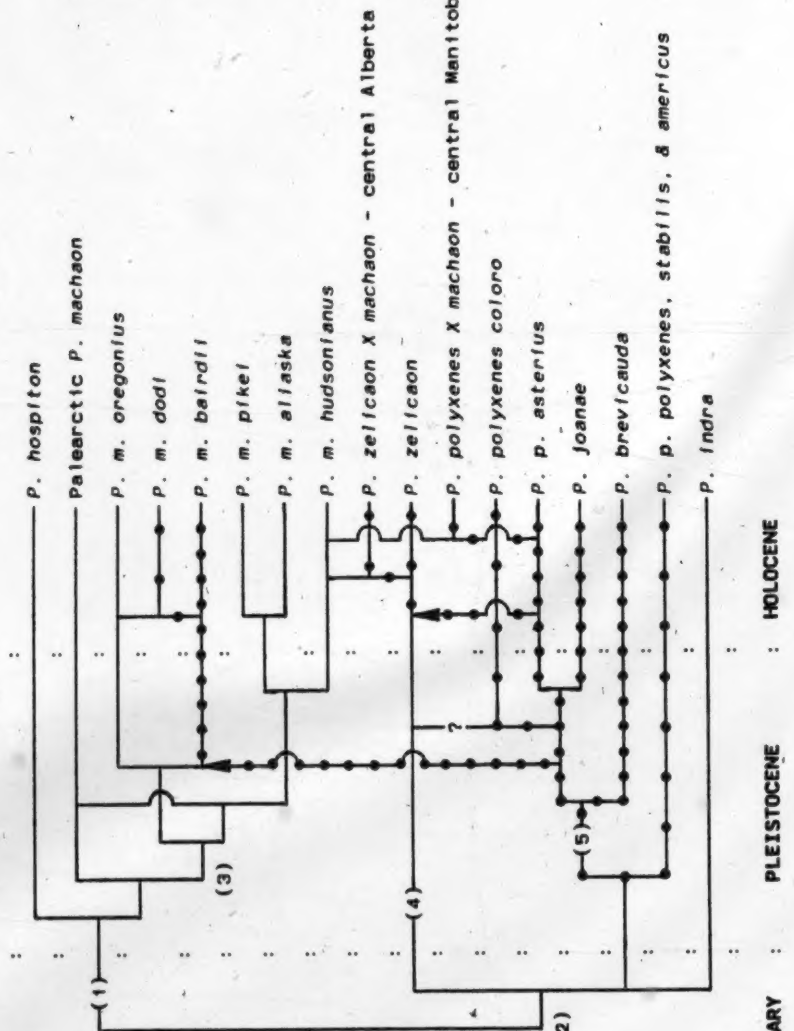
Table 15. Character state distributions within *P. machaon* group taxa

Frequency: X = most common, + = greater than 10%, - = less than 10%
Adult morph.: Letters and numbers correspond to those of characters on Table 2.
Adult electr.: Only alleles with a frequency of more than 10% in at least one taxon are included. Allele letters correspond to those in Table 8. Character polarities not shown due to absence of outgroup information.
Larval: Spot color (sp) = orange (o) & yellow (y). Foodplants (fd.) = Rutaceae (r), Umbelliferae (u) & Compositae (c)
Misc. abbrev.: P = primitive, D = derived, c.AB = central Alberta, c.MB = central Manitoba

CHARACTER SUITE	Adult Morphometric											Adult Electrophoretic								Larval	
CHARACTER NUMBER OR LETTER	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.	K.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
CHARACTER NAME	DHW yel.	DHW pup.	DHW b/r	teg ula	VFW disc	VFW tip	VHW or.	tho rax	abd. VL	abd LL	abd. UL	G6PD	ID	ME	ODH	E4	E5	P1	P2	sp	fd.
STATE or ALLELE	1234	1234	123	123	1234	123	1234	123	1234	123	1234	abkc	bd	iab	abc	ab	ac	ab	ab	oy	ruc
P. hospiton	+X-	+X	X	X	X-	X	X+	X	X	X	X									X	X
Palearctic *P. machaon* ssp.	+X+-	X+	X+-	X	X-	X	X+	X	X	X	X									X	+X-
P. m. oregonius	-+X+	-X-	X++	X	X+-	X	+X-	X	X-	X	X	- X	X+	++X	-X	X	+X	X	+X	X	X
P. m. dodi	+X+	-X+-	-+X	X-	++X	X	-X--	+X-	+--X	X--	-X	---X	X+	-+X	-X	X-	+X	X-	+X	X-	X
P. m. bairdii	X++	X+	-+X	X+	-+X	X+	-X--	++X	---X	++X	X+-+									X+	X
P. m. pikei	X++	+X-	X+-	X	X	X	X+	X	X	X	-X	---X	X-	+X	X-	X-	X+	X+	-X	X+	X
P. m. aliaska	X-	X+	X+	X	X-	X	+X	X	X	X	+X	-- X	X+	-+X	-X+	X-	-X	X+	-X	-X	X
P. m. hudsonianus	X-	+X-	-+X	X	X--	X	+X	X-	X	X	+X+	-- X	X+	-+X	+X-	X+	-X	X+	-X	X	X
P. zelicaon X *machaon* -c.AB	X+-	-X+-	-+X	X-	+++X	X-	-X--	+X+	+--X	X-+	--+X	-+-X	X+	--X	+X-	X+	+X	X+	+X	+X	X
P. zelicaon	X++-	-+X	-X	X-	-+X	X	-X--	X+	--X	X--	--X	-X-+	X-	--X	-X-	-X	-X	X-	+X	+X	+X
P. polyxenes coloro	X++-	-+X	X	+X+	X	X++	+X+	+X	X	+-X	X+--									?X	X-
P. polyxenes X *machaon* -c.MB	X-	X++	-+X	+X+	--X	++X	-+X	--X	---X	--X	X--	+- X	X+	++X	-X	X-	+X	X	XX	-X	X
P. p. asterius	X	-+X	X	+X	X	-X	X	X	X	X	X	X	X	-+X	X	X	X	X	X-	+X	-X
P. joanae	X	+X	X	-X	X	-X	X	X	X	X	X									-X	X
P. brevicauda	X	-+X	X	X-	X	+X-	X	X	X	X	X	X+ +	X	++X	X	X+	X	X	-X	-X	X
P.p.polyx.,stabilis &americus	+X+	+X	X	X++	--X	X++	X	-X	--X	-+X	X+-									X+	-X
P. indra	X-	-+X	-X	X+-	X	-X	X+	X	X	X+	X									X+	X
CHARACTER POLARITY	DPDD	DPPD	DDP	PDD	DPPD	PDD	PPDD	PDD	PDDD	PDD	DDDP									PD	PPD

Figure 40. Reconstructed phylogeny of *P. machaon* group. Location of numbers shows hypothesized first appearance of derived states. Letter and number codes are the same as on Table 2 and 15. Dotted line represents spread of modifier gene for black wing morph. Widely spaced dots indicate low proportion of black morph individuals or incompletely linked gene combinations.

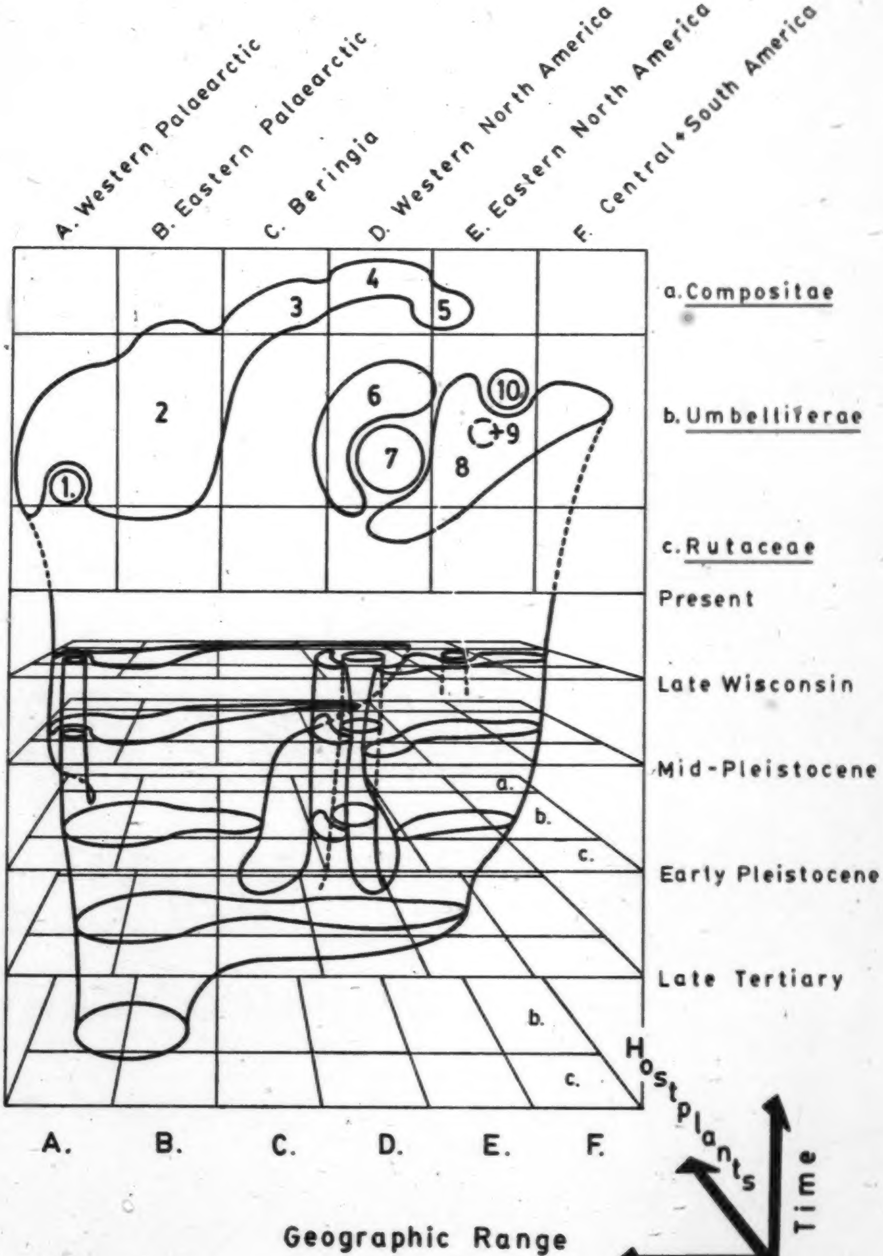
1. B1, C1, E1
2. A1, B4, E4, H2, I4
3. 10c
4. no autapotypies among characters analyzed
5. D3, F3, G4, H3, J3, K1


P. hospiton
Palearctic P. machaon
P. m. oregonius
P. m. dodi
P. m. bairdii
P. m. pikei
P. m. aliaska
P. m. hudsonianus
P. zelicaon X machaon - central Alberta
P. zelicaon
P. polyxenes X machaon - central Manitoba
P. polyxenes coloro
P. p. asterius
P. joanae
P. brevicauda
P. p. polyxenes, stabilis, & americus
P. indra
(1)
(2)
(3)
(4)
(5)
?
TERTIARY
PLEISTOCENE
HOLOCENE

40

Figure 41. Changes in geographic range and larval hostplants over time.

1. *P. hospiton*
2. Palearctic *P. machaon* ssp.
3. *P. m. aliaska*
4. *A. dracunculus*-feeding ssp. of *P. machaon*
5. *P. m. hudsonianus*
6. *P. zelicaon*
7. *P. indra*
8. *P. polyxenes*
9. *P. joanae* (not shown in Late Wisconsin)
10. *P. brevicauda*


A. Western Palaearctic
B. Eastern Palaearctic
C. Beringia
D. Western North America
E. Eastern North America
F. Central + South America
a. Compositae
b. Umbelliferae
c. Rutaceae
Present
Late Wisconsin
Mid-Pleistocene
Early Pleistocene
Late Tertiary
1.
2
3
4
5
6
7
8
9
10
a.
b.
c.
b.
c.
A.
B.
C.
D.
E.
F.
Geographic Range
Hostplants
Time

41

P. machaon and *P. hospiton*.

The relationships of the three lineages which originated in North America are unclear. *P. zelicaon* possesses few if any autapotypic characters, and could conceivably represent the earliest of the three clades to diverge, but shows little internal differentiation. Although the color pattern of adults of *P. p. asterius* is probably highly derived, *P. polyxenes* contains other races and forms (particularly in *P. p. americus*) which appear to be more primitive and similar to *P. zelicaon*. *P. indra*, on the other hand, appears to share some apotypic character states with some *P. polyxenes* subspecies (Table 15), but shows considerable internal differentiation, and has distinctive adult genitalia and adult and larval color patterns. Though this degree of differentiation may indicate an early divergence time relative to the other species, it may also be a reflection of a different sort of selection regime. In fact, it is conceivable that *P. indra* is so different only because some factor such as the distinctive genitalia may have allowed it to completely avoid hybridization and introgression with other species, even though the lineage may be no older than the other three. Since it seems plausible that all three lineages could have diverged at the same time (in West Coast, American southwest, and eastern refugia), I have left this portion of the reconstructed phylogeny as a trichotomy.

There are two main reasons why phylogenetic relationships within the *P. machaon* group are obscure. The group is ecologically very flexible and capable of specific adaptations to local conditions, often through reversals such as a larval host switch to rutaceous plants. The ecological flexibility of the *P. machaon* group has allowed a few species to occupy such large geographic ranges that events such as multiple budding off of peripheral populations from a central population are likely. Reticulation due to interspecific hybridization is also likely to have been a significant factor in the evolution of the group. For example, the black wing morphs of *P. zelicaon* and *P. machaon* are probably due to the introgression of genes from *P. polyxenes*, while large hybrid populations of two of the three potential combinations are described in this study. Both reticulation and multiple peripheral isolation events in variable species are likely to produce discordant character distributions, with resultant difficulties in the reconstruction of their phyologenetic relationships. In the *P. machaon* group these factors are compounded by the fact that the importance of morphometric differences between species is difficult to assess, due to extensive intraspecific variation and the presence of supergenes which affect several characters simultaneously.

6.2 Pleistocene Divergences Within Major Lineages

The first dispersal of the *Papilio machaon* group into North America almost certainly took place across the Beringian region between eastern Siberia and Alaska. Matthews (1978) described a variety of land connections through the Beringian region during the Tertiary, with an increasing potential for biotic exchange toward the end of that period. The Beringian land bridge was also intermittently exposed during the Pleistocene, and formed an important biotic dispersal corridor during that time.

The large scale glacial advances and retreats that occurred throughout the Pleistocene have probably been the most important factor in the differentiation of new species and races. These glaciations, combined with dramatically altered climates, moved many vegetation associations far south of their present ranges and caused the formation of some vegetation associations which have no modern analogs (Matthews 1982). Since most of Canada was covered by ice during glacial advances, the resident *P. machaon* group populations must have been displaced a number of times before returning during warmer periods. Glaciations would have completely isolated Beringian and Asian populations from the populations which survived south of the ice in North America. Glaciations could also have caused major fragmentation of populations within ice free areas by causing habitat changes.

6.2.1 The *P. machaon* lineage

The *P. machaon* lineage now contains only one species other than *P. machaon* itself. This is *P. hospiton*, which must have become isolated on Sardinia and Corsica very early in the history of the lineage. Rumbacher and Seyer (1979) estimated that this happened during the Mindel glaciation, which is the second of the four major glacial periods recognized in Europe. The rest of the *P. machaon* lineage occupied most of the Palearctic region, apparently giving little opportunity for any populations to develop into anything other than distinct regional races.

The Pleistocene glaciations were probably especially important to the acquisition of composite-feeding habits by larvae of *P. machaon* (Figure 41). Since North America was occupied early in the history of the *P. machaon* species group, any later invasion of North America by *P. machaon* may have been inhibited by a prior occupation of most of the available umbellifer-feeding niches by the resident species. This kind of displacement would have been similar to that seen in *P. zelicaon* and *P. polyxenes*, which appear to be parapatric over a considerable distance.

Considering the degree of differentiation present in the *Artemisia*-feeding subspecies, the invasion of this niche must have occurred before the Sangamon Interglacial. The foodplant shift probably occurred in Beringia, when the local populations began to feed on *Artemisia arctica*, a species which is still the main foodplant of *P. machaon* in

Beringia, and is much more abundant than any umbellifer species in the region. The shift would have been aided by several similarities in secondary plant compounds between plants of the genus *Artemisia* and those belonging to the Umbelliferae (Dethier 1941; Berenbaum, 1983). The plant assemblage of the arctic steppe tundra (Matthews, 1982) was probably very similar to that which presently exists in the dry, cold climate of northern Afghanistan, which is the only region in Eurasia in which *P. machaon* has been recorded on *Artemisia*. It is uncertain whether the later switch of *P. machaon* to *Artemisia dracunculus* in North America occurred in Beringia or farther to the south, during a warming trend which allowed Beringian populations to come into contact with dryland habitats characteristic of more southerly latitudes. In any event, the switch to *A. dracunculus* allowed *P. machaon* to occupy large regions in sympatry with *P. zelicaon*, *P. indra*, and, in part, *P. polyxenes* (Figure 41 and 43).

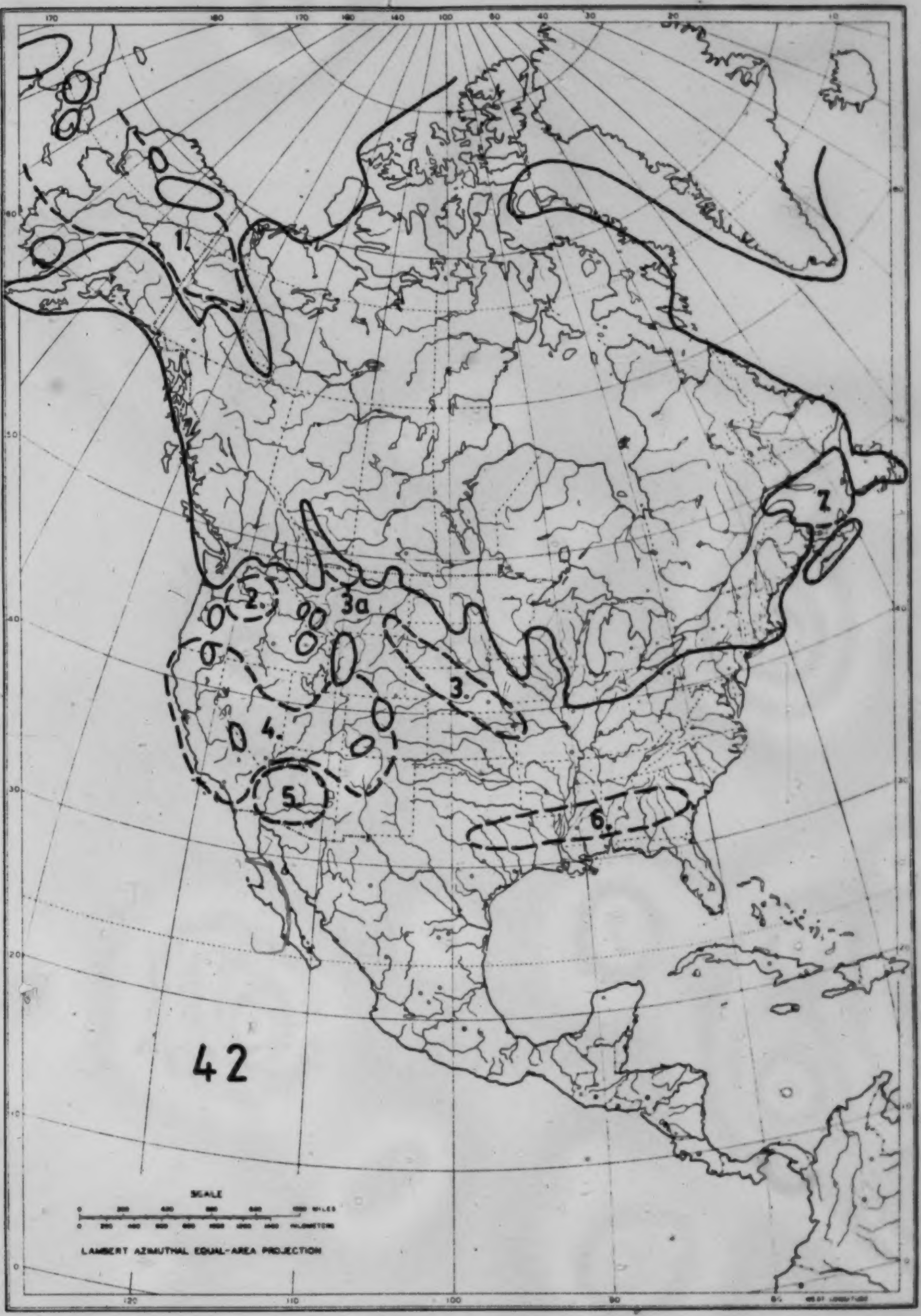
A major factor in the North American differentiation of *P. machaon* would have been contact with *P. polyxenes*. Introgression or even more widespread hybridization just after contact with *P. polyxenes* is probably the reason why *P. m. bairdii* acquired the allele for the the black morph adult (Figure 40). Support for this suggestion may be derived from the marked similarity between artificial hybrids of *P. machaon* and *P. polyxenes*, and the naturally occurring black morph of *P. m. bairdii*. Though the black

Figure 42. Locations of late Wisconsinan refugia. Figure is based in part on Scudder (1978:159). Continuous lines indicate ice masses. Broken lines show refugia hypothesized for *P. machaon* group taxa in the United States and Canada:

1. *P. m. aliaska*
2. *P. m. oregonius*
3. *P. m. hudsonianus*

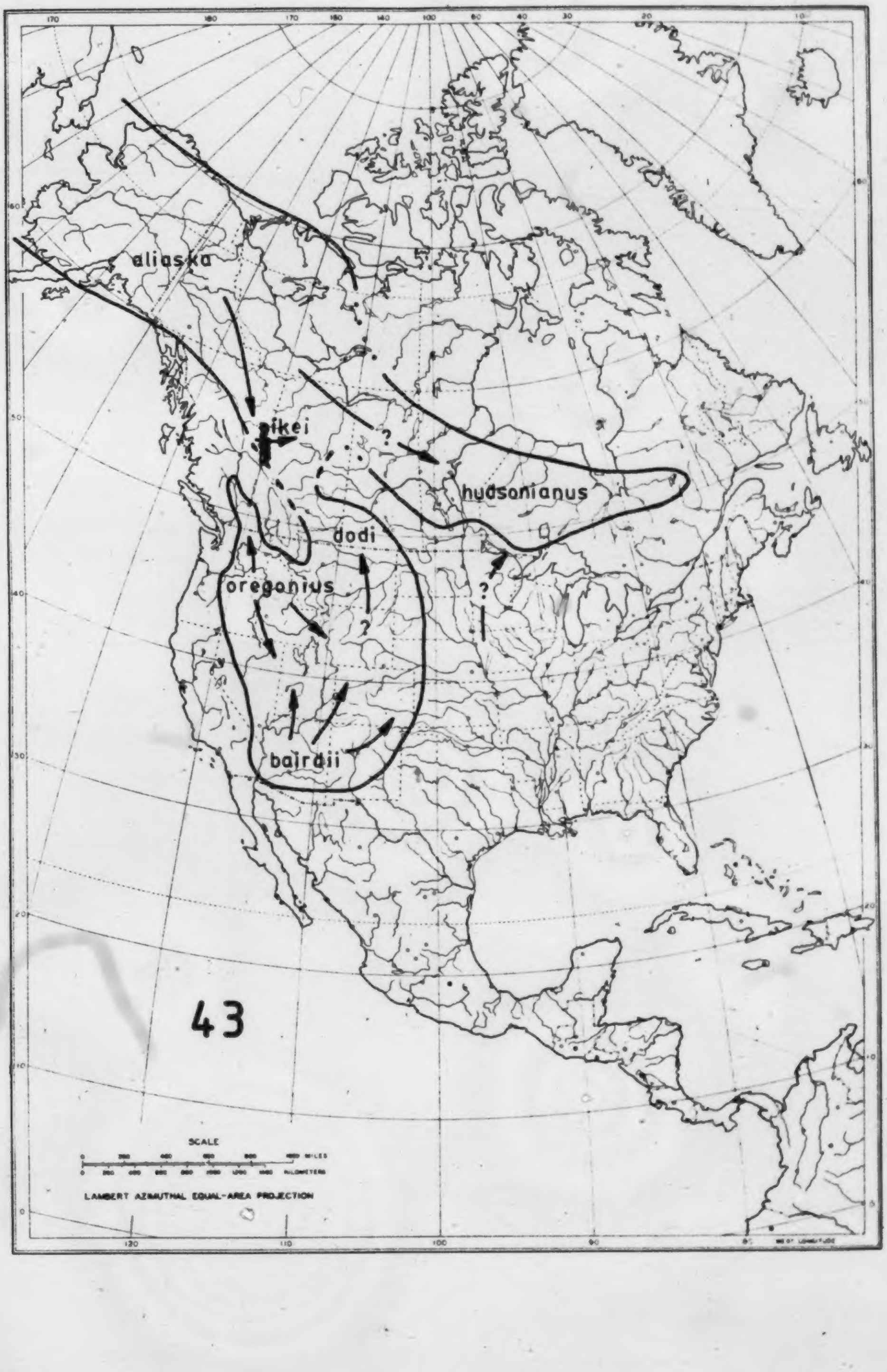
3a. *P. machaon* populations similar to *P. m. hudsonianus*. Remnants present in *P. zelicaon* X *machaon* hybrid populations in central Alberta.

4. *P. zelicaon*
5. *P. m. bairdii* and *P. p. coloro*
6. *P. p. asterius* and *P. joanae*(?)
7. *P. brevicauda*


1.
2.
3.
3a
4.
5.
6.
7.
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
100
90

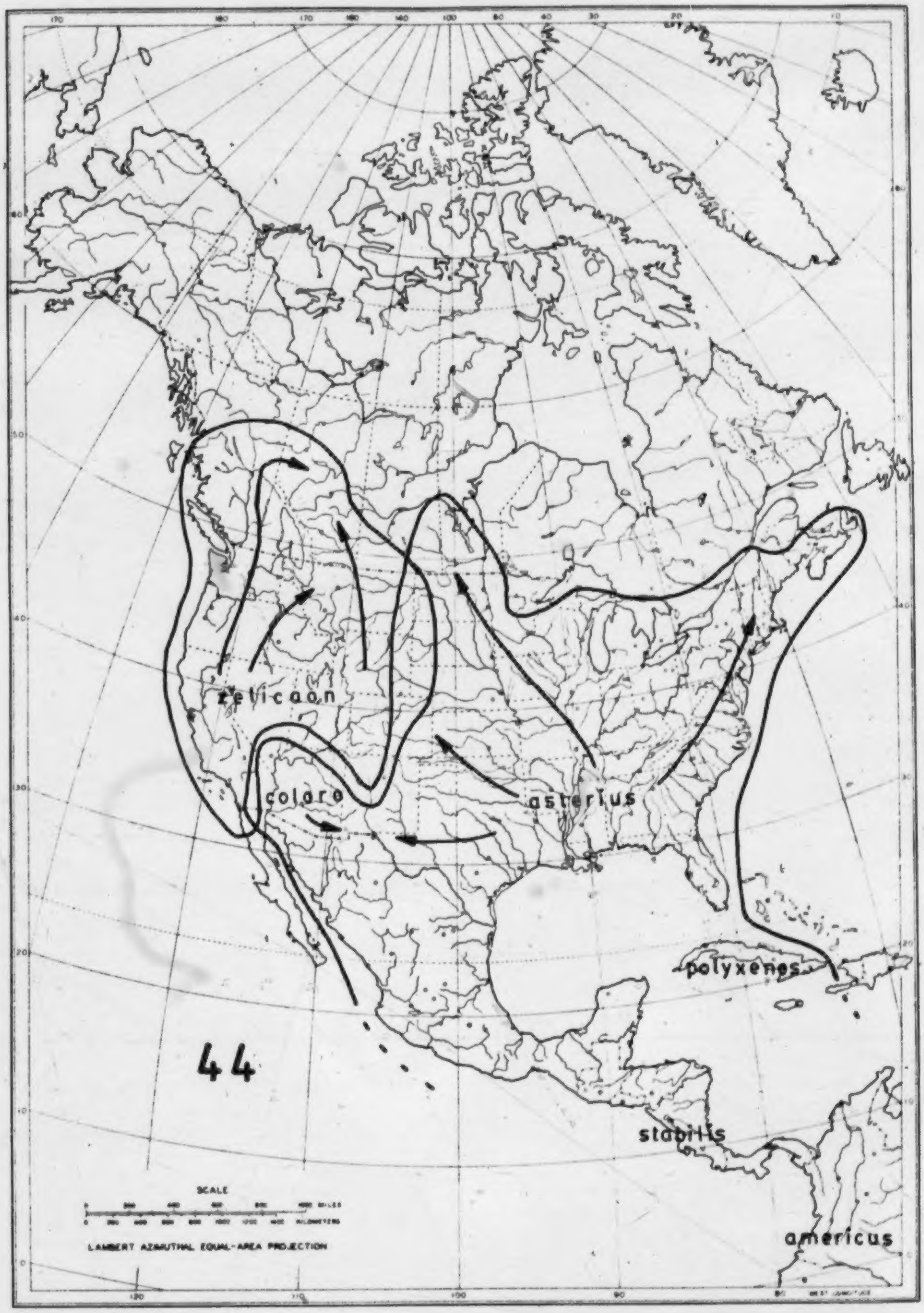
42

Figure 43. Distribution of *P. machaon* in North America. Arrows show hypothesized Holocene dispersal routes.


aliaska
pikei
?
hudsonianus
dodi
oregonius
?
?
bairdii
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

43

Figure 44. Distribution of *P. zelicaon* and *P. polyxenes*. Arrows show hypothesized Holocene dispersal routes in North America.


zelicaon
coloro
asterius
polyxenes
stabilis
americus
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

44

morph of *P. machaon* may also be found some distance from the nearest *P. p. asterius*, it is restricted to a region where either past contact or allele movement through introgression can account for its occurrence.

During late Wisconsinan time, around 18000 years before present, *P. machaon* must have survived in North America in several different refugia (Figure 42). *P. m. aliaska* was restricted to the northernmost refugium, though it may have had a range almost as broad as it has now, including extensions into eastern Siberia. The Beringian refugium may have had an unusually high productivity and diverse fauna during this time, and almost certainly was drier than at present (Hopkins *el al*, 1982). When the glaciers melted, *P. m. aliaska* was able to disperse southward, along recently vegetated areas on the eastern ranges of the Rocky Mountains to Hudson Hope (Figure 43), and may have extended south to the northern Rockies in Alberta once. At present, *P. m. aliaska* is essentially parapatric with *P. zelicaon* in the Rockies, and hybridization between the two species is limited in this region.

The origin of *P. m. hudsonianus* is uncertain. The subspecies now ranges to Quebec, but is very uncommon west of Saskatchewan. This suggests that it diverged from *P. m. aliaska* before the late Wisconsinan, and occupied the boreal region south of the ice during the last major glaciation (Figure 42).

The *A. dracunculus*-feeding populations were more fragmented. The stock that *P. m. bairdii* is derived from probably survived in the remnants of desert habitats in the American southwest, and it seems likely that *P. m. oregonius* is derived from a separate population. This is suggested by the fact that *P. m. oregonius* has no black form like the one which is predominant in *P. m. bairdii*. Although most vegetation reconstructions show only conifer forest grading into tundra at the edge of the glaciers in the northwestern United States, I suggest that the most likely Wisconsinan refugium for *P. m. oregonius* is along the eroding banks of the Columbia River, between Washington and Oregon. Though very close to the ice, the steep north bank of the river must have had a much drier climate than the surrounding region, much like that presently characteristic of the Peace River region. It is even possible that there were dry-tundra adapted *P. machaon* populations along the southern edge of the ice in Washington during the Wisconsinan glaciation, giving rise to *P. m. oregonius* separately from *P. m. bairdii*.

A potential refugium for *P. m. dodi* is even more problematical than for *P. m. oregonius*. Most vegetation reconstructions for the northern Great Plains agree that the region was covered by conifer forest during the late Wisconsinan. It is possible that *P. m. dodi* survived on eroding river banks in the drier areas, or even near the Nebraska Sand Hills. However, if *P. m. hudsonianus* also survived south of the ice, it would probably have had some contact with *P. m. dodi*, and yet *P. m. dodi* has a distinctively darker wing and body coloration. A more likely alternative is that *P. m. dodi* did not exist as a distinctive population during the late Wisconsinan, and arose as a hybrid between *P. m. oregonius* and *P. m. bairdii* when these two populations contacted each other during the Holocene (Figure 39). This would account for the somewhat intermediate adult color pattern of *P. m. dodi*, though not for the fact that the larvae have only orange spots rather than a mixture of orange and yellow. A second explanation is that the dark adult coloration in *P. m. dodi* is due to introgression from *P. zelicaon* in founding populations.

P. m. pikei has probably had a separate origin from the *A. dracunculus*-feeding subspecies which range into the western United States. Although almost all of the butterfly species that are found with it in the Peace River grasslands are clearly derived from conspecific populations in southern Alberta, (E.M. Pike and F.A.H. Sperling - in preparation), *P. m. pikei* is more unlike *P. m. dodi* than any other *P. machaon* subspecies in western Canada. *P. m. pikei* shows a much greater phenetic similarity to *P. m. oregonius* in southern British Columbia. However, it is unlikely that *P. m. pikei* has been derived from *P. m. oregonius*, since none of the available pollen core evidence (eg. Hansen, 1949, 1950, 1955; Valentine, 1980; White and Mathews, 1982) suggests that the grassland vegetation of interior British

Columbia extended across the Rocky Mountains during the Holocene.

I believe it likely that *P. m. pikei* arose during the Holocene from *P. m. aliaska*. If the larger size and more pointed wings are discounted as recent adaptations convergent with other ecologically similar races of *P. machaon*, then the greatest morphometric similarity is with *P. m. aliaska*, or perhaps *P. m. hudsonianus*. *P. m. pikei* has an unusual combination of electrophoretic character states, perhaps due to sampling error or genetic drift in the original colonists, but is slightly more similar to *P. m. aliaska* than to any other *P. machaon* subspecies (Table 8). The most westerly populations of *P. m. pikei* are presently found about 25 km from the nearest alpine *P. m. aliaska* populations, and the strictly univoltine emergence and long daylength requirement for diapause termination are clearly adaptations to a northern habitat.

The most likely time of divergence for *P. m. pikei* is between 8000 and 11000 years B.P.. The ice free section of the foothills east of the Rockies had a periglacial climate at about 11,250 B.P., which was dominated by *Artemisia* and grasses (Schweger *et al*, 1981). However, between 9000 and 6000 B.P. the climate was much hotter and drier than at present, allowing a major expansion of grassland habitats. The relatively rapid shift from dry tundra to hot grassland may have been an important factor in the differentiation of *P. m. pikei* on the Peace River grasslands.

6.2.2 *P. zelicaon* and hybrids

P. zelicaon represents a lineage similar in age to the *P. machaon* and *P. polyxenes* lineages, and yet shows much less tendency toward the development of geographic races. The reason for this may be that its range has not been fragmented much by Pleistocene glaciations and habitat changes. *P. zelicaon* probably occupied a large proportion of the western United States even during the late Wisconsinan maximum (Figure 41), and its range may have bisected that of the *A. dracunculus*-feeding populations of *P. machaon*.

During the post-Wisconsinan climatic amelioration, *P. zelicaon* would have expanded its range northward mainly in mountainous habitats and wet lowlands. However, the species also moved onto the western edge of the Great Plains. The allele for the black adult morph was probably acquired through introgression with *P. p. asterius* early in the Holocene (Figure 40). *P. zelicaon* extended its range into Alberta from two separate directions (Figure 44). One dispersal route was along the foothills and edge of the Great Plains, and brought the allele for the black morph to the prairies and southern foothills of Alberta. The other disperal wave occupied all of British Columbia and spread into Alberta through low mountain passes. It colonized the Peace River region and the northern part of central Alberta.

The two-pronged dispersal of *P. zelicaon* into Alberta seems to have effectively isolated a pre-existing population of *P. machaon* in the foothills of central Alberta. Since most remnants of this population presently occur in forested areas south of Cadomin, the population probably was not associated with the alpine refugium discussed by Pike (1980). This *P. machaon* population came in direct contact with *P. zelicaon* on all sides and may have had a relatively low population density, much like *P. m. hudsonianus* populations in northern Saskatchewan and Manitoba. A significant number of individuals must have begun to hybridize with those of the invading *P. zelicaon* and eventually formed hybrid populations along the ecotone between montane forest and southern grassland in central Alberta. The contention that the hybrid swarm is predominantly derived from hybridization between *P. zelicaon* and boreal populations of *P. machaon* similar to those of *P. m. hudsonianus* is supported by the similarity of the most *P. machaon*-like specimens to *P. m. hudsonianus* rather than to *P. m. dodi*. This similarity includes wing and body pattern characters such as the tendency toward yellow coloration and the presence of a dorso-lateral row of spots on the abdomen, as well as electrophoretic characters such as the high proportion of additional alleles at the ODH locus.

The formation of hybrid populations in central Alberta may have occurred gradually over several thousand years. However, the process appears to have stabilized before the region was affected by agricultural disturbances about 100 years ago. I have seen several specimens collected by F.H. Wolley Dod (1901, 1908) around the turn of the century at the "Head of Pine Creek" and these are identical to the hybrid swarm specimens which I have collected in the same area during the last decade.

The hybrid populations which have arisen on the Cypress Hills may have a different origin from those in the foothills of central Alberta in that they have arisen through persistent hybridization between *P. zelicaon* and *P. m. dodi*. The Cypress Hills *P. machaon X zelicaon* hybrids are very similar to many of the hybrid specimens from the southern part of the central Alberta hybrid region, and yet do not show any of the more extreme *P. machaon*-like characters present in central Alberta. Another possibility is that the Cypress Hills hybrid swarms' genome is simply composed of a higher proportion of *P. zelicaon* genes than in central Alberta. The absence of *P. m. hudsonianus*-like traits may be due to a greater degree of genetic swamping. Some evidence in allele distributions of *Pinus contorta* suggests that the Cypress Hills may have been a refugium during the most recent glaciation (Wheeler and Guries, 1982). If so, then there may even have been a *P. machaon* population on the Cypress Hills during glaciation.

6.2.3 *P. polyxenes* and hybrids

P. p. asterius has a range approximately as extensive as that of *P. zelicaon* (Figure 44) and shows a similar amount of phenotypic and ecological variation. However, *P. polyxenes* includes several other subspecies and two other species have arisen from the same lineage (Figure 40). The additional *P. polyxenes* subspecies range from the American southwest to northern South America and tend to have a more primitive phenotype expressed in the adults and larvae. They are probably phylogenetically older than the related species in the *P. polyxenes* lineage.

The other species in the *P. polyxenes* lineage include *P. joanae*, which appears to be a taxon with only slight (and dubiously significant) differences from *P. polyxenes*. Also included is *P. brevicauda*, a species restricted to the seashore rim in maritime Canada, which probably survived the late Wisconsinan on the exposed ocean shelves in this region (Figure 42, Matthews, 1979). Adults of both of these species have a wing pattern very similar to *P. p. asterius* and must have achieved reproductive isolation from *P. p. asterius* in the late Pleistocene at the earliest. The gene for the black adult wing morph probably originated in the early Pleistocene, but underwent significant modification during the early history of the *P. polyxenes* lineage, after the divergence of the southern subspecies (Figure 40).

P. p. asterius probably survived the late Wisconsinan in the ecotone between woodland and grassland in the southern part of the eastern and central United States (Figure 42). During post-glacial times this race would have extended its range northward to southern Canada (Figure 44). However, *P. p. asterius* may have had a smaller range and a lower population density before North America was settled by

Europeans during the past three centuries (Feeny *et al* 1985). It is now found mostly in successional habitats such as old fields and vegetable gardens. It probably reached Nova Scotia only about 60 years ago (Ferguson, 1954), and still seems to be expanding its range in agricultural regions in central Manitoba and Saskatchewan. *P. p. asterius* must have contacted *P. zelicaon* much earlier in the Holocene or even the late Pleistocene, for the black morph on the eastern edge of *P. zelicaon* to have spread several hundred kilometers beyond the range of *P. polyxenes*.

It is doubtful that *P. p. asterius* had any significant amount of contact with *P. m. hudsonianus* during the late Wisconsinan glaciation, even if both survived in refugia within a few hundred kilometers of each other. They presently are allopatric over most of their range, though hybridization has been extensive where they contact each other in central Manitoba. This hybridization shows signs of not yet having reached an equilibrium, since *P. m. hudsonianus* and the most *P. machaon*-like hybrid forms have become much less common in Riding Mountain Park during the past 50 years.

6.3 Modes of Speciation

Race formation in the *P. machaon* group seems to occur fairly quickly, with ecologically and even phenetically distinctive populations differentiating in a matter of a few thousand years or even a few hundred years under exceptional circumstances. This process has certainly been aided by the very labile genome of the *P. machaon* group, as well as the numerous major climatic changes that have occurred during the Pleistocene. Recent race formation seems to have taken place both at the edge of and in the middle of the range of widespread taxa, when slightly different new larval foodplant resources became available and were opportunistically colonized by individuals from the adjacent population. The most obvious examples include the Peace River race of *P. machaon* and the populations of Californian *P. zelicaon* whose larvae feed on introduced foodplants. Other examples of race formation have probably involved fragmentation of larger populations and subsequent tracking of changes in biome composition in response to changing Pleistocene climates. The *Artemisia*-feeding habits of *P. machaon* in Afghanistan have probably been developed in this manner. A third mechanism may involve interbreeding between previously differentiated populations and the colonization of new geographic regions by the phenetically intermediate populations. This may account for the origin of *P. m. dodi*, though there is as yet little evidence in support of the hypothesis.

The formation of reproductively isolated species seems to have taken much longer than the formation of ecological races, and was probably the result of the adaptation of geographically isolated populations to successively more different habitats. Speciation in the *P. machaon* group usually takes place gradually over hundreds of thousands of years. The low species diversity of the *P. machaon* group in the Palearctic region, despite the formation of many geographic races, suggests that speciation can not occur unless there is an extended period of geographic allopatry. However, even if two populations have been separated for enough time to speciate, hybrid populations may still form between separate species. The process is probably dependent on the degree of ecological difference between the two populations when they meet.

A major factor in expansion and differentiation of new species is the presence of other species. If the two species have undergone substantial genomic differentiation, but a major habitat or larval foodplant shift has not occurred in one of the species, then the two would occupy parapatric ranges. They may exchange some genes but retain their separate genetic integrity. The interaction between *P. zelicaon* and *P. p. asterius* is an example of this. If the populations on either side of a zone of parapatry have developed a slightly different integrated gene complex, then hybrids may be less viable and the zone will be a kind of gene sink. Ecological adaptations such as mechanisms for diapause determination are examples of this in the *P. machaon* group. Hybrids between *P. zelicaon* and *P. machaon* (see phenology section) or *P. polyxenes* (Oliver, 1969) may emerge at a time which is not only different from both of the parental species but is also likely to be inappropriate to the local habitat conditions. Considering the many interrelated factors that are associated with larval foodplant and phenology, speciation and race formation probably involve a major reorganization of polygenic balances (*sensu* Carson, 1981).

In the *P. machaon* group two mechanisms allow more than one species to occupy the same geographic region. One is through the development of functionally different genitalia and hilltopping behavior, together with at least partially different habitat requirements. *P. indra* is an example, and occupies a large part of the western United States in sympatry with *P. zelicaon*, despite the fact that members of both feed on a variety of umbelliferous foodplants. The second mechanism allowing sympatry is for one species to shift to a completely different larval foodplant. *P. machaon* has employed this mechanism to allow it to occupy the same range as *P. zelicaon* in most of western North America. In Arizona and southeastern California the machanism has allowed the greatest local species diversity anywhere within the range of the *P. machaon* group. Here larvae of *P. indra* feed on umbellifers, those of *P. machaon bairdii* feed on composites, and *P. polyxenes coloro* larvae have switched back to a more ancestral foodplant group, the Rutaceae.

6.4 Natural Hybridization

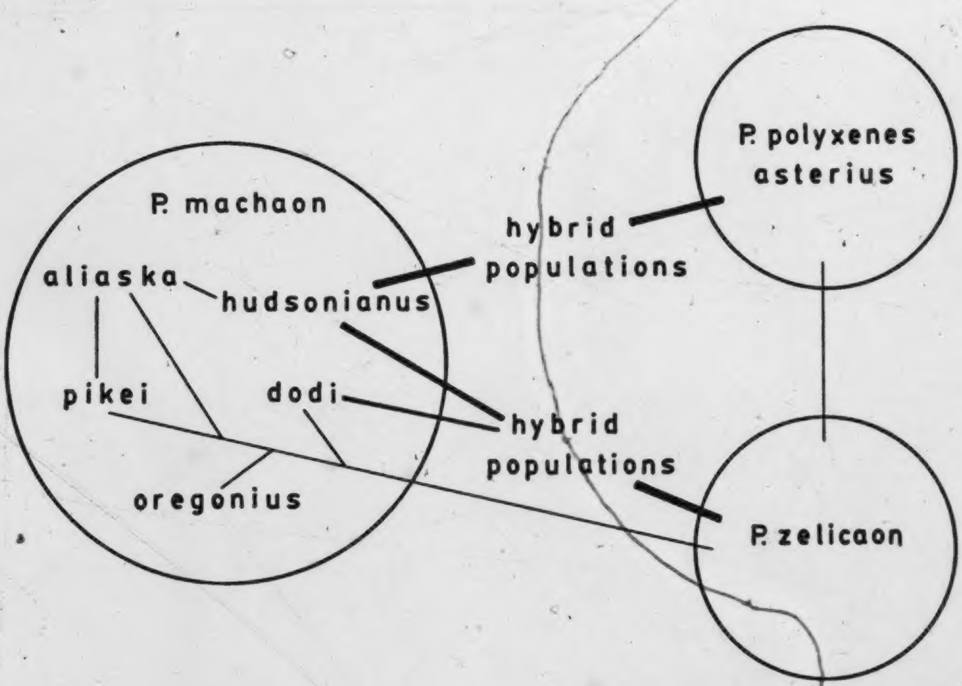
Hybridization between closely related species is a well known event in both plants and animals. The phenomenon is, by definition, in conflict with the biological species concept. Most animal taxonomists deal with this by describing hybridization as interspecific only if hybrids are rare in comparison with the parental forms. However, there are species pairs in which hybridization may be relatively common and yet the parental species maintain their integrity. The species in such a taxonomically difficult group are termed semispecies by some authors, while the group itself may be termed a superspecies (Mayr, 1963). The term semispecies is appropriate for the species in the *P. machaon* group, since these are more reproductively isolated than geographic subspecies and yet hybridize relatively freely in comparison to most other species.

Under some conditions, hybrids are especially common. Such conditions include habitat disturbance, of which the most common source is the clearing of forests by man. However, increased rates of hybridization generally take place in very restricted geographic areas. If hybridization occurs along a narrow line of contact between parapatric species, then such an area is referred to as a hybrid zone. Hybrid individuals may comprise small or large proportions of populations in hybrid zones, and may also be present in varying frequencies within larger areas of overlap between parental species. The species of the *P. machaon* group in western Canada show a low but persistent rate of hybridization in most areas where they come into contact, and in some areas have formed populations in which hybrid individuals are numerically dominant (Figure 45).

6.4.1 Hybrid zones

The zone of hybridization between two species may vary in width from a few hundred meters to more than a hundred kilometers, but is much narrower than the total range of the parental species (Barton and Hewitt, 1981 & 1985). Most hybrid zones are much longer than they are wide, and some span an entire continent. In the *P. machaon* group, the best examples of hybrid zones are along the periphery of the range of *P. polyxenes*. In the American West this species replaces *P. zelicaon* along major ecotones. Although there appears to be several hundred kilometers of overlap between the species, this is due to an interdigitation of habitats and the real hybrid zone is much narrower. It involves a replacement over a few dozen kilometers of *P. polyxenes* by *P. zelicaon* in wetter habitats and higher altitudes. A similar pattern also applies to the transition from *P. polyxenes* to *P. m. hudsonianus* in cooler habitats in Manitoba, though the width of the real zone of intergradation between the two species remains uncertain. In both comparisons, the zones are relatively wide compared to other animals, probably because of the good dispersal powers of *Papilio* butterflies (Shields, 1967).

Figure 45. Hybridization of *P. machaon* group species in western Canada during recent time. Circles indicate species. Relative thickness of lines is proportional to rates of hybridization.


P. machaon
aliaska
hudsonianus
pikei
dodi
oregonius
hybrid populations
hybrid populations
P. polyxenes asterius
P. zelicaon

45

The influence of environmental factors on the location of major hybrid populations is supported by the coincidence of the *P. zelicaon* X *machaon* populations in central Alberta with ecological boundaries and hybrid zones in other species. For example, the southern limit of the hybrid populations in southern Alberta occurs very near to the southernmost limit of many boreal elements. Black spruce (*Picea mariana* [Mill.]BSP) is found in Alberta only as far south as Bragg Creek, while three butterfly taxa characteristic of spruce bogs are also found south to near Bragg Creek. These include *Colias gigantea gigantea* Strecker, *Oeneis jutta chermocki* Wyatt, and *Erebia disa* (Thunberg). The northern limit of the *P. machaon X zelicaon* hybrid populations in central Alberta also coincides generally with the location of several hybrid zones in unrelated taxa. An example is the hybrid zone between *Pinus contorta* and *P. banksiana*, (with a corresponding contact zone between the pine-feeding butterflies *Incisalia eryphon* (Boisduval) and *I. niphon* (Huebner), - Reist, 1979). I am not aware of any animal taxa which form self reproducing hybrid populations within Alberta. However, in plants there is a wide ranging hybrid swarm in the genus *Betula*, which has a distribution very similar to that of the *P. machaon X zelicaon* swarms in central Alberta (Dugle, 1966).

Some hybrid zones appear to have moved a few dozen kilometers within the last century (eg. McDonnell *et al*, 1978). However, such movement is uncommon, and most hybrid zones appear to remain relatively stationary over long periods of time. In fact, hybrid zones probably become trapped in regions of low density, such as habitat clines and natural barriers (Barton, 1979). They may also become narrower, especially if there is strong selection against hybrids, or they may widen and eventually result in the merging of the two parental species. In the *P. machaon* group, there is evidence to suggest that some hybrid zones may presently be undergoing change. This is probably because these zones are very recent, having been influenced by human settlement patterns. The range expansion of *P. polyxenes* into Nova Scotia and Manitoba is probably related to deforestation by man, and so it seems likely that any interaction of this species with *P. brevicauda*, in the east, and *P. m. hudsonianus*, in the west, is less than a century old. The decreasing proportion of *P. machaon* in Riding Mountain Park in Manitoba is thus probably a result of genetic swamping by recently arrived *P. polyxenes* in agricultural areas.

Many hybrid zones have been described for both plants and animals, and most of these zones appear to be the result of secondary contact between formerly allopatric species (eg. Remington, 1968b; Barton and Hewitt, 1985). However, a few hybrid zones may be the result of *in situ* differentiation on either end of a sharp environmental gradient (Endler, 1977). Most authors do not believe that they can distinguish between these two situations, though

Thorpe (1984) states that a phylogenetic analysis at the population level makes such distinctions possible. In the *P. machaon* group it seems most likely to me that most, if not all, of the hybrid zones can most parsimoniously be explained as the result of post-Pleistocene range expansions. However, if *P. m. hudsonianus* spent the late Wisconsinan south of the continental ice sheet, then there may have been a pattern of contact between *P. m. hudsonianus* and *P. p. asterius* which was similar to that found at present. The contact zone between *P. zelicaon* and *P. m. aliaska* is certainly the result of secondary contact.

Hybrid zones which show substantial gene flow are generally no longer considered to represent interspecific hybridization, but rather zones of contact between different races of a single species. Examples include subspecies within both *P. machaon* and *P. polyxenes* in the western United States. However, the degree of gene flow has only been indirectly interpreted from morphological and ecological character gradients and could bear rechecking against enzyme allele distributions. In particular, it should be interesting to compare the rate of gene flow between *P. p. asterius* and *P. p. coloro* in New Mexico with that between *P. p. coloro* and *P. zelicaon* in southern California. Enzyme data for western Canada show a significant interruption in gene flow between *P. machaon* and *P. zelicaon* in most regions in Alberta and British Columbia.

The evolutionary importance of interspecific hybridization is not clear, though various authors have suggested that gene introgression provides an important source of allelic variation for natural selection to act upon. However, most studies of gene flow in hybrid zones show only limited intrusions of alleles into neighboring species (Barton and Hewitt, 1985). The black morph in the *P. machaon* group generally follows this pattern as well, though it has moved several hundred kilometers into the range of *P. zelicaon* and has displaced the yellow allele in the southern part of the range of *P. machaon*.

The selective advantage of alleles which produce the black adult morph is unknown. Since many populations are polymorphic with respect to this allele, it is probably not important as a visual mechanism for mate recognition, as Hafernik (1982) reported for an analogous wing pattern in *Junonia* (Nymphalidae). It may give hilltopping males an advantage in maintaining a position at the very peak of hills (Scott, 1983 and personal observations). However, Miller (1977) suggested that the allele is lethal when homozygous and in combination with the *P. zelicaon* genome. Perhaps the distribution of the allele is the result of an equilibrium between positive and negative selection, much as hybrid zones themselves may be a balanced conflict between genes that widen zones by reducing incompatibilities and genes that narrow zones by producing reproductive isolation (Barton and Hewitt, 1981).

6.4.2 Hybrid populations

Some populations in interspecific hybrid zones are characterized by negative or neutral selection on hybrid individuals in the contact zone. However, hybrid populations are characterized by positive selection for interspecific hybrids in restricted areas, even though the parental species retain their integrity over most of their area of contact. Hybrid populations are composed predominantly of hybrid forms, and variation within most such populations spans the full range of phenotypes between the parental forms. In a fully integrated hybrid population, individuals phenotypically similar to parental forms simply represent the phenotypic extremes within the population.

Hybrid populations are reasonably common in plants, where they are often referred to as hybrid swarms, but are very unusual in animals (Mayr, 1963; Grant, 1977). Most animal examples are of birds, amphibians and fish, and the studies of Sibley (1954) on towhees and those of Blair (1941) and others on toads are still among the best documented. Insect examples are much less common, and all of those that I am aware of have a preponderance of hybrid forms along a broad area of contact, indicating that the species involved are not reproductively isolated, or have only a minority proportion of hybrid forms at any given locality.

The present study provides the clearest example in butterflies, and perhaps even in insects, of hybrid populations between broadly sympatric species. In the *P. machaon* group the best examples of hybrid swarms are the *P. machaon X zelicaon* populations in central Alberta, particularly the one at Bragg Creek. The Bragg Creek population is composed of a highly varied but unimodal population which is almost completely made up of hybrid forms, and probably has no significant internal impediment to gene flow. The intermediate nature of the central Alberta populations is indicated by both the morphometric and electrophoretic character distributions.

Hybrid populations very frequently appear to be associated with habitat disturbance of some sort, which creates a kind of hybrid habitat in which forms intermediate between the parental species can flourish. Since there has been a great deal of habitat disturbance by man in recent times, there have been several opportunities to observe the formation of new hybrid swarms over a period of only a few decades (eg. Gillespie, 1985). An interesting aspect of some hybrid populations is that they separate again into parental forms within about 20 years (Jones, 1973; Corbin *et al*, 1979). Considering the ephemerality and dependence on habitat disturbance of many hybrid swarms, the examples of the *P. machaon* group from central Alberta are fairly unusual. They occur in areas with relatively little or no habitat disturbance, especially compared to the regions dominated by agriculture where *P. machaon* and *P. zelicaon* coexist with only a small amount of hybridization. As well, material collected around 1900 suggests that the hybrid populations were already in existence when central Alberta was first being settled.

Although artificial hybrids within the *P. machaon* group have invariably been obtained between individuals from geographically distant populations, and many showed substantial infertility even when they were from interspecific populations clearly connected by character clines, some backcrosses to either of the parental species have produced viable adults (Clarke and Sheppard, 1953; Ae, 1966; Clarke et al 1977). In a few crosses, adults have even been obtained from an F2 hybrid cross of *P. polyxenes* and *P. zelicaon* (Ae, 1964). These experiments indicate that introgression and the formation of hybrid swarms are at least possible, though unlikely. However, at least part of the inviability of hybrids is due to environmental adaptations, such as diapause characteristics (Oliver, 1969). Since the three species in western Canada are very flexible in their adaptation to different environmental factors, it is reasonable to expect that species coming together in a particular region tend to be more similar than would populations from more distant regions. Unless some fundamentally different adaptation has occurred, such as a major shift in larval foodplant and habitat, parapatric populations seem likely to meet and hybridize on a continuing basis, until some form of reproductive isolation occurs. Thus the reason for the formation of *P. machaon X* *zelicaon* hybrid swarms in central Alberta is probably related to similarities in the habitat preferences of local races before contact occurred through range expansions. The two species coexist where *P. machaon* larvae feed on *Artemisia* and where adult contact is reduced through the occupation of different habitats. Where *P. machaon* occupies a habitat more similar to that of *P. zelicaon*, as does *P. m. hudsonianus*, the two species have tended to merge, with the hybrid populations feeding on plesiotypically palatable umbellifers. This situation is similar to that described by Mayr (1963) for *Passer domesticus* (Linneaus) and *P. hispaniolensis* Temminck in Europe.

Many plants form hybrid swarms, and the frequency with which such events occur may be related ecological characteristics of particular taxa (Raven, 1976). Many species of trees, shrubs and perennials have only slightly developed internal barriers to hybridization. Such plants tend to maximize the saturation density (K) of their populations and are separated by ecological and other extrinsic factors. However they can still hybridize with related species to form new recombinants, which allow populations to adapt to changing environments. On the other hand, species whose populations maximize their rate of increase (r), such as annual herbs, tend to hybridize much less frequently with each other. Since they are characterized by rapid dipersal and growth in new areas, as well as a high commitment of basic resources to reproduction, barriers to hybridization are much more important to these species. This correspondence between maximization of saturation density and tendency toward hybridization in plants does not seem to apply to the *P. machaon* group. These butterflies would, if anything, be considered as maximizing their rate of increase, since they feed in the larval stage on successional plants and are dependent on rapid colonization and foodplant exploitation.

The evolutionary significance of hybrid swarm formation is uncertain. It may be rare enough in animals so that it has had little influence on evolutionary patterns. However, it may be that such breakdowns in reproductive barriers contribute to the formation of new populations under conditions in which one of the parental species would have been eliminated by habitat destruction. In this way part of the threatened gene pool is saved, albeit in a greatly altered combination. The formation of hybrid populations may also cause a major disorganization of the polygenic balances of the parental species, leading eventually to speciation through a major new balanced genetic system (Carson, 1981).

New species that may have arisen from interspecific hybrid swarms would be impossible to detect by morphological features if the hybridization occurred between a sibling species pair. On the other hand, if the new species is the product of hybridization between species A and C, and there exists a species B which is more closely related to A than C is, then the hybrid origin of the new species would be indicated by its discordant character distribution. Unfortunately, as Mayr (1963) pointed out, such a character distribution could also easily be due to the character convergences and parallelisms which one would expect in closely related species with a very similar basic gene pool. For these reasons, the number of animal taxa which have had a hybrid origin has almost certainly been underestimated, and will continue to remain so until there has been ample opportunity to support or reject present taxonomic assignments with independent character suites, such as enzyme alleles.

A major strength of the present study is that the general pattern of morphometric character states has been checked against distribution of electrophoretic character states. Such character congruence indicates that the observed patterns are probably of biological significance to the animals themselves. As well, this congruence lends support for the use of both color pattern and electrophoretic characters in systematic studies.

7. CONCLUDING STATEMENTS

There is considerable potential for future research on the *P. machaon* group. Much of that potential lies in study of the genetics of speciation. However, in order to put understanding of genetic interactions among taxa of the *P. machaon* group on a firmer footing, the phylogenetic relationships of the group should first be thoroughly re-examined with new characters, such as enzyme alleles. As well, there is a need for a broad survey of species interactions in the American southwest, similar to that which I have provided for western Canada.

A number of color pattern and electrophoretic markers are available for study of the genetic integration of hybrid populations in the *P. machaon* group. The most obvious of these markers, the black adult color morph, could easily be investigated for behavioral aspects of selection regimes. An interesting further step would be to compare the distribution of these markers, which are probably controlled by nuclear genes, against that of cytoplasmically inherited genes, as was done by Ferris *et al* (1983) for a hybrid zone in mice.

Clarke and Sheppard (1955b) stated that "It is clear that the Machaon-group provides some of the most suitable material ever investigated in animals for studying the process of speciation in detail, taking into account genetic, ecological and behaviour differences as well as time". I agree wholeheartedly with this view, since the wide genotypic variation present within the group makes genetic investigations relatively tractable.

However, study of the *P. machaon* group is also interesting because the variety of hybrid interactions poses conceptual problems in understanding the nature and origin of species. Such hybrid interactions "contrast two views of the species: as a set of populations delimited by genetic barriers to gene exchange; and as a set of populations maintained in a particular stable equilibrium by selection" (Barton and Hewitt, 1985). The appropriateness of study of the *P. machaon* group to an examination of species concepts is illustrated by the fact that Hagan (1882) and Edwards (1883) expressed similar opposing views a century ago.

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Appendices: Tables 16-20

Table 16. Specimens used in initial PCAs.

LOCALITIES (grouped by regions)	COLLECTION DATES	NUMBERS and SEX
Southern and Central British Columbia		
Abbottsford (from H. Kimmich)	reared 1982	3m 7f
Kootnay Smt., 40 km w Creston	reared 1982	1f
Bear Lake, 75 km n Prince George	reared 1982	1f
Macalister, n Williams Lake	18 Aug. 1982	1f
Soda Creek area	reared 1982	2m 2f
Savona	reared 1982	2f
Kamloops area	reared 1983	25m 23f
Peace River Region of British Columbia (BC) and Alberta (AB)		
Pink Mt., BC (alpine)	5-7 July 1981	2m
Pink Mt., BC (alpine)	5-7 July 1982	26m 5f
Pink Mt., BC (alpine)	reared 1982	1m 2f
Alaska Hwy. Mile 150 (boreal)	7 July 1982	2m
Butler Ridge, BC	8 July 1981	6m
Attachie, BC	reared 1981	7m 2f
Taylor, BC	9 July 1981	1m
Taylor, BC	21 June 1982	12m 4f
Taylor, BC	8 July 1982	8m 1f
Taylor, BC	reared 1982	1m
Clayhurst Ferry, BC	reared 1980	1f
Clayhurst Ferry, BC	reared 1981	1m
Clayhurst Ferry, BC	reared 1982	12m 6f
11 km w Dawson Creek, BC	21 June 1982	6m
47 km w Dawson Creek, BC	reared 1982	1m 1f
50 km w Dawson Creek, BC	2 July 1982	1m
Quint. Mt., 105 km s Dawson Cr., BC	20 June 1982	1m 1f
Thunder Mt., 90 km s Dawson Cr., BC	3 July 1981	1m
Thunder Mt., 90 km s Dawson Cr., BC	20 June 1982	15m
Thunder Mt., 90 km s Dawson Cr., BC	9 July 1982	5m
Thunder Mt., 90 km s Dawson Cr., BC	reared 1982	1m 1f
Kleskun Hills, ne Grande Praire, AB	19 June 1982	1m
Kleskun Hills, ne Grande Praire, AB	reared 1981	1f
21 km w Valleyview, AB	9 July 1982	1f
21 km w Valleyview, AB	reared 1982	1m 1f
18 km w High Prairie, AB	reared 1983	1f
Spirit Ridge, 16km s Spirit R., AB	9 June 1982	4m
Spirit Ridge, 16km s Spirit R., AB	19 June 1982	1m

Table 16. Continued

Dunvegan, AB	22 June	1982	- 3m	1f
Dunvegan, AB	reared	1982	-	1f
Highland Park, AB	14 June	1981	- 7m	
Highland Park, AB	9 June	1982	- 5m	
Shaftesbury Ferry, AB	reared	1980	-	1f
Peace River, AB (town)	13 June	1981	- 4m	
Peace River, AB (town)	reared	1980	- 1m	
Peace River, AB (town)	reared	1981	-	1f
Twin Lks., 60 km n Manning, AB	reared	1983	- 1m	
Central Alberta				
Marten Mt., n Lesser Slave Lk.	1-2 June	1981	- 6m	
Marten Mt., n Lesser Slave Lk.	11 July	1981	- 1m	
Marten Mt., n Lesser Slave Lk.	7 June	1982	- 1m	
Marten Mt., n Lesser Slave Lk.	11 June	1982	-11m	2f
Marten Mt., n Lesser Slave Lk.	19 June	1982	- 2m	
Marten Mt., n Lesser Slave Lk.	1 July	1982	- 3m	
Pelican Lkt., 45 km n Calling Lk.	31 May	1981	-	1f
House Mt., 35 km s Kinuso	2 June	1981	-	1f
Goose Mt., w Swan Hills	11 July	1981	- 4m	
Goose Mt., w Swan Hills	18 June	1982	-17m	
e Fox Creek	reared	1982	-	1f
10 km e Clyde	2 June	1981	- 3m	
10 km e Clyde	10 June	1982	- 1m	
Lake Eden, 35 km w Edmonton	4 June	1982	- 1m	
Athabasca Lkt., w Hinton	22 June	1981	- 1m	
Rock Lake, 30 km nw Hinton	reared	1982	-	1f
Adams Lkt., Wilmore Park	11-12 July	1982	- 4m	2f
Baldy Lkt., n Nordegg	16 June	1982	- 1m	1f
30 km e Nordegg	reared	1982	- 4m	
Buck Mt., ne Buck Lake	5 June	1981	- 2m	
Buck Mt., ne Buck Lake	29 May	1982	-13m	
Buck Mt., ne Buck Lake	4 June	1982	-19m	
Buck Mt., ne Buck Lake	17 June	1982	-13m	3f
Buck Mt., ne Buck Lake	reared	1982	- 5m	5f
Buck Mt., ne Buck Lake	9 June	1983	- 8m	
10 km se Rimbey	reared	1982	-	1f
13 km w Sylvan Lake	reared	1982	-	1f
7 km e Lacombe	16 June	1982	- 3m	
7 km e Lacombe	26 June	1982	- 1m	
Antler Hill, 16 km s Red Deer	9 June	1983	- 5m	
Blue Hill, 40 km w Sundre	25 June	1981	- 4m	
18 km w Cochrane	24 June	1981	- 1m	
5 km s Bragg Creek	4-5 June	1981	- 4m	
5 km s Bragg Creek	24 June	1981	- 1m	
5 km s Bragg Creek	3 June	1982	- 1m	
5 km s Bragg Creek	15 June	1982	- 8m	
5 km s Bragg Creek	2 Aug.	1982	- 1m	
5 km s Bragg Creek	reared	1982	-12m	13f
5 km s Bragg Creek	9-10 June	1983	-32m	

Table 16. continued

Southern Alberta (AB) and Saskatchewan (SK)

Waterton National Park	reared	1981 - 3m	4f
Waterton National Park	reared	1982 - 5m	1f
5 km n Spring Coulee	reared	1983 -	4f
18 km n Taber	15 May	1982 - 4m	3f
18 km n Taber	6 Aug.	1983 - 3m	1f
18 km n Taber	reared	1983 - 6m	3f
Wintering Hills, 18km s Drumheller	24-5 May	1982 - 9m	
Wintering Hills, 18km s Drumheller	30 May	1982 - 2m	
Wintering Hills, 18km s Drumheller	1 June	1982 - 3m	1f
Wintering Hills, 18km s Drumheller	29 May	1983 - 4m	1f
Wint. Hills, 10km s East Coulee	31 May	1982 - 2m	
Wint. Hills, 10km s East Coulee	1 June	1982 - 3m	
Wint. Hills, 10km s East Coulee	8 Aug.	1982 - 4m	
Wint. Hills, 10km s East Coulee	29 May	1983 -11m	
Dorothy	reared	1980 -	1f
Dorothy	reared	1982 -	1f
Rosedale, 3 km e Drumheller	2 June	1982 - 2m	1f
Drumheller (town)	reared	1981 - 1m	1f
Drumheller (town)	31 May	1982 - 9m	1f
Drumheller (town)	1 June	1982 - 3m	
Drumheller (town)	14 June	1982 - 7m	
Drumheller (town)	30 June	1982 - 6m	1f
Drumheller (town)	8 Aug.	1982 - 4m	
Drumheller (town)	29 May	1983 -15m	
Drumheller (town)	reared	1982 - 6m	6f
2 km sw Nacmine	reared	1980 -	1f
2 km sw Nacmine	10 May	1982 - 1m	
2 km sw Nacmine	1 June	1982 -16m	
Hand Hills, 12 km s Delia	31 May	1982 - 5m	
Hand Hills, 12 km s Delia	29 May	1982 - 3m	
Bleriot Ferry, w Munson	1 June	1981 - 1m	
Bleriot Ferry, w Munson	30 May	1982 -	1f
Morrin Br. (Hwy. 27 Junc.)	reared	1980 -	1f
Tolman Bridge, 15 km e Trochu	reared	1981 -	1f
Tolman Bridge, 15 km e Trochu	reared	1982 - 5m	
Nevis Junction	reared	1982 - 3m	3f
Nose Hill, 22 km ne Coronation	14 June	1982 - 2m	
Saskatchewan Landing Prov. Park, SK	28 May	1983 - 3m	
Outlook, SK	reared	1982 - 6m	1f
Outlook, SK	28 May	1983 - 4m	

Manitoba (MB), Wisconsin (WN) and Ontario (ON)

Thompson, MB	1-2 July	1983 -32m	5f
Duck Mt. Park, MB (from Troubridge)	reared	1982 - 3m	5f
Gladstone, MB	reared	1983 - 1m	1f
Caledonia, WN (from J. Daniels)	reared	1983 -11m	4f
Owen Sound, ON (from J. Cumming)	reared	1983 - 1m	
Caledonia, ON (from J. Troubridge)	reared	1982 - 2m	3f

Table 17. PCA loadings for morphometric characters.

Characters	No. of states	Prescaling factor	Morph. char. alone PCA 1	Morph. char. alone PCA 2	Morph. char. alone PCA 3	Morph. + E4 char. PCA 1	Morph. + E4 char. PCA 2	Morph. + E4 char. PCA 3	Morph. char. Discr. axis 1	Morph. char. Discr. axis 2
1. DHW anal yellow exent	4	0.67	-.08802	.12724	.27738	-.08372	.02764	.08635	-.95632	.44984
2. DHW eyespot pupil shape	4	0.67	.28135	.19610	.10183	.26693	-.05769	-.03854	2.6312	.27348
3. DHW anal red/blue separ.	3	1.00	.37599	.27346	.80043	.27261	.16605	.22422	.14586	.55359
4. Tegula color	3	1.00	.07436	-.33219	.11648	.03302	.19600	-.15353	---	---
5. VFW discal yellow	4	0.67	.51509	.06374	-.28744	.37299	.20126	.20876	.39570	.43740
6. VFW apical yellow smudge	3	1.00	.08838	-.41026	.09393	.03637	.22296	-.13920	-2.7946	1.6308
7. VHW postmedian orange	8	0.30	.14498	-.28593	.16419	.08924	.19921	-.06422	.66918	-1.0964
8. Metathoracic yellow	3	1.00	.36657	-.17656	-.15262	.25103	.23432	.05245	.28560	-.45912
9. Abdominal ventral line	9	0.25	.56179	.15238	-.29493	.40858	.19615	.26391	-.06198	.35159
10. Abdominal lateral line	3	1.00	.12509	-.48817	.09946	.05888	.26658	-.17854	.13832	1.1457
11. Abdominal upper line	9	0.25	-.08016	.46195	-.14093	-.02775	-.24319	.16434	-1.1759	3.5709
% Variance :			54.65	69.77	78.23	32.15	44.41	52.43	89.92	100.00

Table 18. PCA loadings for electrophoretic characters.

		E4 Char. alone			E4 + morphometric char.		
	RF	PCA 1	PCA 2	PCA 3	PCA 1	PCA 2	PCA 3
1. Est.4 -A	.48	.51272	.15272	-.02904	-.33301	.36403	.05708
2. Est.4 -B	.54	-.51272	-.15272	.02904	.33301	-.36403	-.05708
3. Est.5 -I	.57	.00281	.00096	.00340	-.00139	.00198	.00387
4. Est.5 -A	.64	.19435	-.08321	.04902	-.13379	.02804	.20182
5. Est.5 -B	.65	.00102	.00627	-.00852	-.00075	.00517	-.01076
6. Est.5 -C	.71	-.18834	.08005	-.04069	.12558	-.03532	-.19735
7. Est.5 -D	.75	-.00984	-.00406	-.00332	.01035	.00013	.00242
8. IDH -A	.16	.01543	.00573	.03868	-.00843	.01350	.03020
9. IDH -B	.18	-.17800	.10887	-.67783	.08152	-.14324	-.49039
10. IDH -C	.20	.01242	-.01002	.04098	-.00276	.01427	.03949
11. IDH -D	.22	.14815	-.10776	.59545	-.06855	.11444	.42063
12. IDH -E	.24	.00200	.00319	.00272	-.00177	.00103	.00007
13. G-6-PD -E	.16	-.00626	-.00620	-.00219	.00418	-.00554	.00054
14. G-6-PD -A	.18	-.00348	-.02464	-.04630	-.00465	-.01925	-.02791
15. G-6-PD -B	.20	-.39512	-.01550	.20452	.26404	-.23216	.00096
16. G-6-PD -I	.22	.02659	.02598	.02329	-.00964	.02352	.02127
17. G-6-PD -K	.24	-.00810	.19082	-.01734	.03584	.16790	-.14632
18. G-6-PD -C	.26	.38743	-.17131	-.20646	-.29287	.05305	.10797
19. G-6-PD -D	.30	.00554	.00044	.04316	.00249	.01211	.04351
20. ME -J	.475	.00054	.01709	-.00127	.00148	.01349	-.01271
21. ME -I	.500	.02200	.05463	-.00671	-.01602	.02571	-.02904
22. ME -A	.525	.11023	.07610	-.05571	-.08679	.02720	-.02777
23. ME -B	.550	-.11791	-.18817	.04522	.08245	-.08608	.07342
24. ME -K	.575	-.00517	.01708	.00738	.00603	.00856	-.00626
25. ME -C	.600	-.01012	.01489	.01263	.01182	.00519	.00700
26. ME -D	.625	.00044	.00839	-.00154	.00103	.00593	-.00465
27. ODH -A	.17	-.02009	-.01992	.00120	.01443	-.01302	.00069
28. ODH -B	.21	.03391	.08377	.06075	-.00636	.07126	.03737
29. ODH -C	.25	-.01382	-.06384	-.06195	-.00807	-.05824	-.03806

Table 18. continued

		E4 Char: alone			E4 + morphometric char.		
	RF	PCA 1	PCA 2	PCA 3	PCA 1	PCA 2	PCA 3
30. MDH -I	.16	-.00416	.00789	.00077	.00311	-.00029	-.00394
31. MDH -A	.18	.00180	-.01337	.01411	-.00061	-.00059	.01346
32. MDH -B	.22	.00073	.00134	-.02392	-.00367	-.00648	-.01371
33. MDH -C	.26	.00163	.00414	.00841	.00116	.00736	.00419
34. aGPD -A	.29	-.00175	-.00103	.00015	.00112	-.00145	.00004
35. aGPD -B	.32	.00133	.00040	.00255	.00040	.00386	.00267
36. aGPD -C	.35	.00042	.00063	-.00271	-.00152	-.00241	-.00271
37. PROT.1 -A	.21	-.06502	.11926	.17948	.08496	.08659	.08444
38. PROT.1 -B	.26	.06502	-.11926	-.17948	-.08496	-.08659	-.08444
39. PROT.2 -I	.300	.00174	.00564	.00360	-.00232	.00019	-.00101
40. PROT.2 -A	.315	-.04194	.61290	.06720	.07296	.27771	-.27535
41. PROT.2 -B	.330	.03746	-.62296	-.07016	-.07021	-.28161	.27537
42. PROT.2 -C	.345	.00274	.00442	-.00063	-.00043	.00370	.00099
% Variance :		31.04	43.18	52.97	32.15	44.41	52.43

Table 19. Larval spot color

Usually only locality samples for which N is greater than 10 are listed.
Abbreviations: yel = yellow; or = orange; c. = circa; AB = Alberta;
AK = Alaska; BC = British Columbia; CA = California; MB = Manitoba;
NWT = Northwest Territories; US = United States; WA = Washington;
YT = Yukon Territory.

Taxon + Locality	Spot Color yel	 or	 %yel	Source
Papilio machaon -includes all wild collected larvae on composites				
P. machaon aliaska				
Pink Mt., BC (alpine)	18	1	94.7	FAHS -1981,1982
Stewart Crossing, YT	1	0		Kimmich-1978 (*in litt.*)
upper Dempster Hwy.,YT	1	0		Kimmich-1981 (*in litt.*)
Brooks Range, AK	"red-orange"			Remington (1967:33)
P. machaon hudsonianus				
Torch Lake, SA	1			Anweiler-1976, photo
P. machaon pikei				
E. of Hudson Hope, BC	27	49	35.5	FAHS -1984
Attachie, BC	11	45	19.6	FAHS -1981
Clayhurst Fy., BC	42	109	27.8	FAHS -1980,81,82
Dunvegan, AB	32	52	38.1	FAHS,Pike -1980,81,82
Peace River, AB	9	55	14.1	FAHS -1980,81
totals, incl. misc. loc.	130	333	27.8	
P. machaon oregonius				
Soda Creek area, BC	18	0	100.	FAHS -1982
Kamloops, BC	71	0	100.	FAHS -1983
Penticton area, BC	17	0	100.	FAHS -1980
southern BC region	"all yellow"			Kimmich 1960-84 (*in litt.*)
Biggs area, Oregon	c.20	0	100.	FAHS -1980
Oregon (?)	yellow			Dornfeld (1980)
near The Dalles, Oregon	yellow			Emmel(1975:394)
"many other localities"	orange			Emmel(1975:394)
30 mi. e. Yakima, WA	mostly yellow, but 2 orange cases seen			- Newcomer(1964)

Table 19. continued.

Taxon + Locality	Spot Color yel	or	%yel	Source
P. machaon dodi				
Nevis Junction, AB	1	25	3.8	FAHS -1981,82,83
Tolman Bridge, AB	0	28	0.0	FAHS -1981,82
Drumheller, AB	1	124	0.8	FAHS,Pike -1980,81,82
East Coulee, AB	0	23	0.0	FAHS -1980,81
Dorothy, AB	0	9	0.0	FAHS -1980,82
Drumheller area, AB	"orange-red"			Emmel (1975:394)
total Red Deer R. area (incl. misc. localities)	2	c.233	0.9	FAHS,Pike -1980 to 83
Calgary, AB	0	2		FAHS -1983
Spring Coulee, AB	0	7		FAHS -1983
Vauxhall, AB	0	c.225	0.	FAHS,Pike -1980 to 83
Outlook, Saskatchewan	0	11	0.	FAHS -1982
P. machaon "brucei"				
Glenwood Springs, Colorado	yellow			Edwards (1895:240)
P. machaon bairdii				
Mingus Mts., Arizona	"orange-yellow"			Bauer (1955)
Arizona (Mingus Mts.?)	orange			Clarke and Sheppard (1956 -from Bauer 1955, and pers. comm.)
s.e. California	orange			Emmel and Emmel (1973)
San Bernardino Mts., CA	"red-orange"			Remington (1967)

Table 19. continued

Taxon + Locality	Spot Color yel	or	%yel	Source
P.zelicaon - includes all larvae on Umbelliferae				
southern BC				
Ucluelet, BC	mostly yellow, some orange			Guppy -1969, pers comm.
Fraser lowland	about 6 yellow to 1 orange			Kimmich -1982, *in litt.*
s. Enderby, BC	13	13	50.0	FAHS -1984
Glacier Park, BC	0	3		FAHS -1984
w. Revelstoke, BC	0	4		FAHS -1984
Peace River region				
Pink Mt., BC (valley)	2	8	20.0	FAHS -1982,84
e. Hudson Hope, BC	0	11	0.	FAHS -1984
w. Ft.St.John, BC	0	22	0.	FAHS -1984
w. Dawson Creek, BC	0	40	0.	FAHS -1982,84
Thunder Mt. Lkt., BC	0	6	0.	FAHS -1982
Wembley, AB	2	15	11.8	FAHS -1984
Woking, AB	0	8	0.	FAHS -1984
Valleyview, AB	6	67	8.2	FAHS -1982,84
Twin Lakes, AB	2	4	33.3	FAHS -1983
totals, incl. misc. loc.	12	186	6.1	
southern Alberta				
Coleman area, AB	7	6	53.8	FAHS -1981
Waterton, AB	65	67	49.2	FAHS -1981,82,83
western US				
Gothic, CO	c.10	0	100.	Remington (1967)
Gothic, CO	35	0	100.	FAHS -1980
western US	yellow and orange at most localities			eg. Clarke and Sheppard (1970), Emmel (1975), Fisher (1981), Remington (1967).

Table 19. continued

Taxon + Locality	Spot Color			Source
	yel	or	%yel	
P.zelicaon X machaon (central Alberta, larvae on umbellifers)				
northern region				
Faust, AB	1	5	16.7	FAHS -1984
e. Slave Lake, AB	0	8	0.	FAHS -1984
e. Fox Creek, AB	0	13	0.	FAHS -1982,84
Switzer Park, AB	0	6	0.	FAHS -1980,81
totals, incl. misc. loc.	1	38	2.6	
central region				
30 km e. Nordegg, AB	1	6	14.3	FAHS -1982
Buck Mt., s.e. Drayton Vy.	10	26	27.8	FAHS -1982
totals, incl. misc. loc.	13	36	26.5	
southern region				
Bragg Creek, AB	42	3	93.3	FAHS -1980,82
P. polyxenes asterias				
southern Ontario	"always yellow"			J. Troubridge -*in litt.* 1984.
conterminous US	yellow or orange, but usu. yellow			eg. Clarke(1932), Clarke and Sheppard (1955, 1970), Dickerson (1901), Emmel (1975), Remington (1967).
P.polyxenes X machaon (central Manitoba, larvae on umbellifers)				
Duck Mts., MB	1	1		FAHS -1980
Riding + Duck Mt. areas	"only yellow"			Troubridge -*in litt.* 1984.
Riding Mt. Park, MB	14	0	100.	FAHS -1980
Riding Mt. Park area, MB	"all yellow"			Kimmich -1981 -*in litt.* 1981.
Gladstone, MB	4	0		FAHS -1983

Table 20. Larval foodplant records.

Only wild collected larvae and confirmed ovipositions under natural conditions are included. Entries are arranged by taxon and region. All entries from a particular locality are grouped together, even though entries from major hybrid zones produced a variety of adults. Uncredited entries refer to personal obsevations or collections. Abbreviations: AB = Alberta, BC = British Columbia, MB = Manitoba, SK = Saskatchewan, NWT = Northwest Territories.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. aliaska				
Pink Mt.(alpine), BC	*Artemisia arctica*	6 July 1981	1 egg	not emg.
Pink Mt.(alpine), BC	*Artemisia arctica*	17 Aug. 1982	4-3rd, 3-4th, 16-5th	1m, 2f
Eagle Summit, Alaska	*Artemisia arctica*	197?	1 egg, K.Phillip (pers.comm. 1983)	not reared
Dawson, Yukon	*Artemisia arctica*	1949	ovip. obs. by P. Bruggeman (Freeman, 1949)	
Richardson Mts., Yukon	*Artemisia arctica*	June 1981	ovip. obs. by J. Troubridge -*in litt*. 1981,	not reared
near Aklavik, NWT	*Petasites palmatus* var. *frigidus*	1931	larvae observed by O. Bryant (Leussler, 1935)	
Arctic Red River, NWT	"small low-growing carroty plant" (?*A. arctica*)	late June 1955	oviposition observed by C. Wyatt (1957)	
P. m. hudsonianus				
Jan Lake, SK	?*Sanicula marilandica*	June 1972	ovip. obs. by G. Anweiler (Hooper, 1973),	not reared
Torch Lake, SK	*Petasites palmatus*	August 1976	1-5th, color photo by G. Anweiler,	not reared
P. m. oregonius				
Penticton area, BC	*Artemisia dracunculus*	20 August 1980	6-1st, 10-2nd, 7-3rd, 14-4th, 15-5th	1m
Penticton area, BC	*A. dracunculus*	1 July 1984	1-3rd, 1-4th	not reared
Macalister-Soda Cr., BC	*A. dracunculus*	18 August 1982	1-1st, 1-3rd, 2-4th, 16-5th, 1 pupa	2m, 2f
Savona, BC	*A. dracunculus*	19 August 1982	1-2nd, 2-5th	2f
Kamloops, BC	*A. dracunculus*	26,27 Aug. 1983	1-e, 2-4th, 15-4th, 56-5th	25m, 23f
Grant Co., Washington	*A. dracunculus*	1 July 1983	"ova & larvae" -Lepidopterists' News (Season Summary 1983)	
Deschutes Park, Oregon	*A. dracunculus*	26 July 1980	14-e, 15-1st, 25-2nd, 12-3rd, 6-4th, 5-5th	no emg.
Biggs, Oregon	*A. dracunculus*	26 July 1980	1-3rd, 1-4th, 6-5th	1f

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. pikei				
12km ne Hudson Hope, BC	*Artemisia dracunculus*	12 July 1984	2-e, 3-1st	no emg.
12km ne Hudson Hope, BC	*A. dracunculus*	20 August 1984	9-4th, 64-5th	22m, 20f
Attachie, BC	*A. dracunculus*	9 July 1981	2-e, 13-1st & 2nd, 1-3rd, 1-4th	1m
Attachie, BC	*A. dracunculus*	9 August 1981	11-4th, 41-5th	9m, 4f
Taylor, BC	*A. dracunculus*	18 August 1980	2-5th	1f
Taylor, BC	*A. dracunculus*	8 July 1982	2-1st, 1-2nd, 1-3rd, 1-4th	1m
8 km e. Ft.St.John, BC	*A. dracunculus*	18 August 1980	1-5th	no emg.
Clayhurst Fy., BC	*A. dracunculus*	17 August 1980	1-4th, 59-5th	3m, 5f
Clayhurst Fy., BC	*A. dracunculus*	9 August 1981	3-4th, 46-5th	3m, 2f
Clayhurst Ferry, BC	*A. dracunculus*	16 August 1982	2-4th, 42-5th	12m, 6f
18 mi w Fairview, AB	*A. dracunculus*	21 August 1980	1-5th	T. Pike -*in litt.* 1980 emg.?
Dunvegan, AB	*A. dracunculus*	13,15,17 Aug.80	4-4th, 24-5th	T. Pike -*in litt.* 1980 emg.?
Dunvegan, AB	*A. dracunculus*	16 August 1980	6-4th, 32-5th	3m, 3f
Dunvegan, AB	*A. dracunculus*	8 August 1981	7-4th, 15-5th	no emg.
Dunvegan, AB	*A. dracunculus*	15 August 1982	1-4th, 4-5th	1f
Dunvegan, AB	*A. dracunculus*	8 July 1984	1-e, 1-1st	(G.J. Hilchie, leg) no emg.
10 mi s.w. Fairview, AB	*A. dracunculus*	19,28 Aug.& 1 Sept.80	10-5th	T. Pike -*in litt.* 1980 emg.?
10 mi s.w. Fairview, AB	*A. dracunculus*	15 August 1982	6-5th	no emg.
Camp I., s. Whitelaw, AB	*A. dracunculus*	15 August 1980	1-4th	1m
Shaftesbury Ferry, AB	*A. dracunculus*	15 August 1980	2-5th	1f
Peace River (town), AB	*A. dracunculus*	14 August 1980	4-4th, 56-5th	2m, 1f
Peace River (town), AB	*A. dracunculus*	8 August 1981	1-4th, 3-5th	1f
Peace River (town), AB	*A. dracunculus*	24 July 1983	1-2nd	no emg.
Peace River (town), AB	*A. dracunculus*	18 August 1984	11-5th	2m, 1f
12 mi e. North Star, AB	*A. dracunculus*	11 August 1981	5-5th	no emg.
Kleskun Hills, AB	*A. dracunculus*	12 August 1981	1-5th	1f

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. m. dodi				
Nevis Junction, AB	*Artemisia dracunculus*	19 August 1981	5-5th	1m
Nevis Junction, AB	*A. dracunculus*	3 Sept. 1982	2-3rd, 2-4th, 17-5th	3m, 3f
Nevis Junction, AB	*A. dracunculus*	8 Sept. 1983	2-5th	no emg.
Tolman Bridge, AB	*A. dracunculus*	30 July 1981	4-5th	2m, 1f
Tolman Bridge, AB	*A. dracunculus*	3 Sept. 1982	1-3rd, 4-4th, 20-5th	5m
Morrin Bridge, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt*. 1980	emg.?
Morrin Bridge, AB	*A. dracunculus*	10 August 1980	2-2nd, 8-5th	2f
Bleriot Ferry, AB	*A. dracunculus*	2nd wk. July 80	c.50-1st & 2nd J. Troubridge -*in litt*. 1980	emg.?
Bleriot Ferry, AB	*A. dracunculus*	10 August 1980	2-4th, 14-5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	22 July 1981	2 larvae -4th or 5th	no emg.
Bleriot Ferry, AB	*A. dracunculus*	20 July 1982	E.M. Pike, pers. comm.	emg.?
Bleriot Ferry, AB	*A. dracunculus*	20 July 1982	1-2nd E.M. Pike, pers. comm.	emg.?
Nacmine, AB	*A. dracunculus*	2nd wk July 80	c.100-1st & 2nd. J. Troubridge -*in litt*. 1980	emg.?
Nacmine, AB	*A. dracunculus*	10 August 1980	2-2nd, 1-3rd, 3-4th, 12-5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	c.11 Aug. 1980	21-4th & 5th E.M. Pike, pers. comm.	emg.?
Nacmine area, AB	*A. dracunculus*	22 July 1981	40 larvae, mostly 4th & 5th	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	19 August 1981	5-5th	emg. counted w. Drumheller
Nacmine area(+ Bleriot)	*A. dracunculus*	19 July 1982	2-2nd(Bler.); 1-3rd, 4-5th(Nac.)	emg. counted w. Drumheller
Nacmine area, AB	*A. dracunculus*	8 August 1982	3-4th, 8-5th	emg. counted w. Drumheller
Hwy 575, w. Nacmine,AB	*A. dracunculus*	22 July 1981	5 larvae, ? instars, 1 pupa	no emg.
Drumheller, AB	*A. dracunculus*	10 August 1980	2-2nd, 1-3rd, 3-4th, 12-5th	2m, 3f
Drumheller, AB	*A. dracunculus*	22 July 1981	15 larvae, mostly 4th & 5th	6f
Drumheller, AB	*A. dracunculus*	19 July 1982	3-1st, 3-2nd, 2-3rd, 6-5th	4m, 5f
Drumheller, AB	*A. dracunculus*	8 August 1982	2-4th, 17-5th	1m, 2f
Drumheller area, AB	*A. dracunculus*	20 July 1982	1-4th, 7-5th E.M. Pike, pers. comm.	emg.?
Drumheller, AB	*A. dracunculus*	3 Sept. 1982	1-4th, 4-5th	no emg.
East Coulee, AB	*A. dracunculus*	2nd wk July 80	250 larvae, mostly 1st & 2nd J. Troubridge -*in litt*. 1980	
East Coulee, AB	*A. dracunculus*	10 August 1980	7-1st, 5-2nd, 8-3rd, 8-4th, 7-5th	no emg.
East Coulee, AB	*A. dracunculus*	22 July 1981	3-larvae, 4th or 5th	no emg.
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	
East Coulee, AB	*A. dracunculus*	19 August 1981	3-4th, 1-5th	no emg.
Dorothy, AB	*A. dracunculus*	2nd wk July 80	48 larvae, mostly 1st & 2nd J. Troubridge -*in litt*. 1980	
Dorothy, AB	*A. dracunculus*	10 August 1980	1-e, 1-1st, 1-2nd, 3-3rd, 1-4th, 3-5th	2m, 1f
Dorothy, AB	*A. dracunculus*	19 July 1982	5-2nd, 1-3rd, 2-5th	1f
Dorothy, AB	*A. dracunculus*	8 August 1982	1-4th	no emg.

Table 20. continued.

Taxon and Locality	**Foodplant**	**Date**	**Instars**	**Adults obtained**
P. m. dodi - continued				
Outlook, SK	*A. dracunculus*	9 Sept. 1982	1-2nd, 1-3rd, 1-4th, 10-5th	6m, 1f
Outlook, SK	*A. dracunculus*	28 May 1983	ovip. observed	not reared
Calgary, AB	*A. dracunculus*	30 August 1983	2-4th	no emg.
Spring Coulee, AB	*A. dracunculus*	29 August 1983	3-4th, 4-5th	4f
Taber Prov. Park, AB	*A. dracunculus*	10 August 1980	1-1st E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	7 August 1980	50 larvae, 2nd to 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	9 August 1980	40 larvae, 2nd to 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	26 August 1980	13-4th, 37-5th	7m, 17f
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 July 1981	c.100 larvae, mostly 1st & 2nd	no emg.
8 mi. s. Vauxhall, AB	*A. dracunculus*	19 August 1981	c.70 larvae, mostly 4th & 5th	17m, 10f
8 mi. s. Vauxhall, AB	*A. dracunculus*	6 July 1982	30 larvae, mostly 5th E.M. Pike, pers. comm.	4m, 3f
8 mi. s. Vauxhall, AB	*A. dracunculus*	8 July 1982	10 larvae, 4th or 5th E.M. Pike, pers. comm.	emg.?
8 mi. s. Vauxhall, AB	*A. dracunculus*	29 August 1983	1-2nd, 1-3rd, 7-4th, 13-5th	6m, 3f
P. m. bairdii				
Canyonlands NP, Utah (Needles District)	*Artemisia dracunculus*	20 May 1985	2-3rd	not reared

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon				
southern & interior BC				
Saanich, BC	*Lomatium nudicale*	1957	G.A. Hardy-leg. specm. in BCPM	1f + 1?m
Francis Peak, BC	*Oenanthe sarmentosa*	8 August 1962	G.A. Hardy-leg. specm. in BCPM	1f
Ucluelet, BC	*Heracleum lanatum*	May & July	2nds to 5ths both months C. Guppy -*in litt*. 1982	
Thetis Island, BC	"garden parsley"	"often"	?instars R. Guppy (1970)	
Abbotsford, BC	*Angelica lucida*	?date	?instars "a major foodplant" -H. Kimmich *in litt*. 1982	
Abbotsford, BC	*Sium suave*	end of Aug. 82	mostly 5ths Kimmich *in litt*. 1982	in FAHS colln: 3m,7f
Abbotsford, BC	*Angelica genuflexa*	end of Aug. 82	mostly 5ths Kimmich *in litt*. 1982	included above
Abbotsford, BC	*O. sarmentosa*	c. 10 Aug. 1984	?instars Kimmich *in litt*. 1984	in FAHS colln: 7m,9f
Abbotsford, BC	*Cicuta occidentalis*	c.10 Aug. 1984	?instars Kimmich *in litt*. 1984	included above
Matsqui, BC	*Sium suave*	July & August	all instars Kimmich *in litt*. 1982	?emg.
Manning Park, BC	*Osmorhiza chilensis*	? date	?instars Kimmich *in litt*. 1982	?emg.
Kootenay Skyway Smt.,BC	*Heracleum lanatum*	20 August 1982	1-3rd	1f
5 km s Enderby, BC	*Heracleum lanatum*	30 June 1984	6-2nd, 2-3rd	incl. w. next entry
5 km s Enderby, BC	*Heracleum lanatum*	2 July 1984	3-2nd, 7-3rd, 1-4th, 7-5th	4m, 1f
11 km w Revelstoke, BC	*Heracleum lanatum*	30 June 1984	1-1st, 4-2nd	3m
Rogers, BC (Glacier NP)	*Heracleum lanatum*	30 June 1984	1-1st, 2-2nd	no emg.
Tete Jeune Cache, BC	*Heracleum lanatum*	26 August 1983	1-5th	no emg.
Barkerville, BC	*Heracleum lanatum*	August	?instar N. Criddle-leg. McDunnough (1927)	1f
Macleod Lake,n PrGeo,BC	*Zizia aptera*	? date	?instars H. Kimmich *in litt*. 1982	?emg.
Bear Lk,n.Prince Geo.BC	*Heracleum lanatum*	18 August 1982	1-5th	1-5th
Peace River region				
Pink Mt.(valley), BC	*Heracleum lanatum*	16 & 17 Aug. 82	5-4th, 3-5th	no emg.
Pink Mt.(valley), BC	*Heracleum lanatum*	19 August 1984	1-3rd, 1-5th	no emg.
10km ne Hudson Hope, BC	*Heracleum lanatum*	12 July 1984	5-1st, 2-2nd, 3-3rd, 1-4th	3m
15 km w Ft.St. John, BC	*Heracleum lanatum*	12 July 1984	6-1st,9-2nd,4-3rd,2-4th,2-5th	no emg.
Cecil Lake, BC	*Heracleum lanatum*	9 July 1984	4-1st, 2-2nd E.M. Pike -pers. comm.	?emg.
30 mi w Dawson Creek,BC	*Zizia aptera*	2 July 1982	1-2nd, 1-3rd, 1-4th	1m, 1f
30 mi w Dawson Creek,BC	*Zizia aptera*	10 July 1984	2-1st	no emg.
40 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	2-1st, 6-2nd, 1-3rd	no emg.
18 km w Dawson Creek,BC	*Heracleum lanatum*	10 July 1984	17-1st, 6-2nd, 3-3rd, 3-5th	1m
w. Chetwynd, BC	*Heracleum lanatum*	18 August 1982	1-5th	no emg.
Thunder Mt., BC	*Heracleum lanatum* & *Angelica genuflexa*	9 July 1982	7-1st, 9-2nd, 4-3rd	1m

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. zelicaon - continued				
14 mi. w. Elmworth, AB	*Heracleum lanatum*	9 July 1982	2-1st, 4-2nd	not reared
3.5 km nw Wembley, AB	*Heracleum lanatum*	10 July 1984	4-1st, 5-2nd, 3-3rd, 2-4th	1m, 3f
3.0 km nw Wembley, AB	*Sium suave*	10 July 1984	1-e, 4-1st	1m
2 km e Woking, AB	*Heracleum lanatum*	8 July 1984	1-1st, 5-2nd, 2-3rd	1f
2 km e Woking, AB	*Zizia aptera*	8 July 1984	2-1st	no emg.
2 km w Debolt, AB	*Sium suave*	12 July 1984	1-5th	1f
13 mi. w Valleyview,AB	*Heracleum lanatum*	9 July 1982	5-2nd, 8-3rd, 18-4th, 22-5th	2m, 1f
13 mi. w Valleyviw, AB	*Heracleum lanatum*	12 July 1984	8-1st,17-2nd,8-3rd,4-4th,6-5th	no emg.
15 mi e High Prairie,AB	*Heracleum lanatum*	27 July 1983	2-3rd	1f
11 mi. s. Dixonville,AB	*Heracleum lanatum*	27 July 1983	1-3rd	not emg.
Twin Lks.(n.Manning),AB	*Heracleum lanatum*	25 July 1983	4-5th, 2-4th	2m
southern Alberta & Saskatchewan				
Coleman area, AB	*Angelica dawsoni*	27 July 1981	3-e, 2-1st, 3-2nd	no emg.
Coleman area, AB	*Angelica dawsoni*	18 August 1981	1-1st, 2-3rd, 1-5th	no emg.
Coleman area, AB	*Angelica arguta*	18 August 1981	1-2nd, 7-3rd, 6-4th, 8-5th	no emg.
9 mi se Beaver Mines,AB	*Angelica arguta*	19 August 1981	1-4th	no emg.
9 mi se Beaver Mines,AB	*Angelica dawsoni*	21 August 1982	1-3rd	no emg.
9 mi se Beaver Mines,AB	*Heracleum lanatum*	21 August 1982	1-5th	no emg.
Waterton Park, AB	*Angelica arguta*	27 July 1981	35 larvae, 1st & 2nd instar	no emg.
Waterton Park, AB	*Angelica arguta*	19 August 1981	c.100 larvae, mostly 5th	6m, 8f
Waterton Park, AB	*Angelica dawsoni*	19 August 1981	1-5th	1m
Waterton Park, AB	*Lomatium dissectum*	19 August 1981	6+ larvae, 4th & 5th	2m, 3f
Waterton Park, AB	*Heracleum lanatum*	19 August 1981	1-5th	no emg.
Waterton Park, AB	*Angelica arguta*	21 August 1982	5-2nd, 5-3rd, 3-4th, 4-5th	1f
Waterton Park, AB	*Angelica dawsoni*	21 August 1982	1-3rd	no emg.
Waterton Park, AB	*Lomatium triternatum*	21 August 1982	1-4th	no emg.
Waterton Park, AB	*Heracleum lanatum*	21 August 1982	3-5th	2f
Waterton Park, AB	*Angelica arguta*	29 August 1983	1-2nd, 4-4th, 15-5th	3f
Waterton Park, AB	*Heracleum lanatum*	29 August 1983	1-5th	no emg.
Eston, Sask.	"garden dill"	September 1955	larvae prod. both yel. & bl. adults - Hooper (1973:65)	
western US				
Gothic, Colorado	*Angelica ampla*	2-3 Aug. 1980	1-1st, 2-3rd, 16-4th, 18-5th	1f

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. machaon X *zelicaon* - Hybrid zone, Umbellifers				
northern region				
Faust, AB	*Heracleum lanatum*	5 July 1984	3-2nd, 3-3rd	2m
22 km e Slave Lake	*Heracleum lanatum*	5 July 1984	5-1st, 2-2nd, 2-3rd	1m, 1f
Fox Creek, AB	*Heracleum lanatum*	10 July 1982	1-1st, 3-2nd, 9-3rd, 7-4th	not reared
Fox Creek, AB	*Heracleum lanatum*	14 August 1982	2-4th, 2-5th	1f
Fox Creek, AB	*Angelica genuflexa*	14 August 1982	1-5th	not emg.
30 km e Fox Creek, AB	*Heracleum lanatum*	13 July 1984	3-1st, 6-2nd, 1-4th	no emg.
7 mi. s. Whitecourt, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Cherhill, AB	*Heracleum lanatum*	10 July 1982	1-5th	no emg.
Ft. Saskatchewan, AB	garden celery	9 August 1984	1-5th	1m
Rock Lake, AB	*Heracleum lanatum*	29 August 1982	4-5th (A. Nimmo, leg.)	1f
3 mi n Moberly Lkt., AB	*Heracleum lanatum*	13 July 1982	2-1st, 3-2nd	no emg.
Switzer Park, AB	*Zizia aptera*	5 July 1980	2-e, 2-2nd, 1-3rd, 1-4th	2m
Switzer Park, AB	*Zizia aptera*	17 July 1981	2-e., 1-2nd	not emg.
Switzer Park, AB	*Zizia aptera*	13 July 1982	1-2nd	not emg.
Switzer Park, AB	*Heracleum lanatum*	13 July 1982	8-1st, 2-2nd	no emg.
Switzer Park, AB	*Heracleum lanatum*	2 Aug. 1982	38-1st & 2nd,2-3rd,2-4th,1-5th:	no emg., T.Pike -pers. comm.
central region				
3 mi. sw. Thorsby, AB	*Heracleum lanatum*	15 July 1982	1-5th	included with Buck Lk.
e. of Buck Lk., AB	*Heracleum lanatum*	16 July 1982	2-2nd, 5-3rd, 6-4th, 27-5th	5m, 5f
Rimbey, AB	*Heracleum lanatum*	16 July 1982	2-4th	1f
7 mi. w. Sylvan Lk.,AB	*Heracleum lanatum*	16 July 1982	1-3rd	1f
19 mi. e. Nordegg, AB	*Heracleum lanatum*	17 July 1982	11-1st, 10-2nd, 1-3rd	4m
2 mi. s. Nordegg, AB	*Heracleum lanatum*	17 July 1982	1-1st	no emg.
4 mi e Elm Cr. Cpgd.,AB	*Zizia aptera*	17 July 1982	1-2nd	
10 mi e Limestone Mt,AB	*Heracleum lanatum*	17 July 1982	1-3rd	no emg.
Didsbury, AB	"parsnip"	? ? 1908	produced 1 m (form *nitra*), in Canadian National Collection	
Waiparous Cpgd., AB	*Zizia aptera*	20 July 1981	4-2nd	no emg.
southern region				
3 mi se. Bragg Creek,AB	*Zizia aptera*	12 & 14 July 80	8 larvae, 1st & 2nd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18 July 1982	1-3rd	no emg.
3 mi se. Bragg Creek,AB	*Zizia aptera*	18July- 7Aug.82	11-1st, 20-2nd, 6-3rd, 4-4th	11m, 13f
Chain Lks. Prov. Pk.,AB	?*Angelica arguta*	18 July 1982	2-3rd T. Pike - pers. comm.	not reared

Table 20. continued.

Taxon and Locality	Foodplant	Date	Instars	Adults obtained
P. polyxenes X *machaon*	- Hybrid Zone			
Somme, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg. & colln. 1m
Weekes, SK	"parsnip"	Sept. 1977	? instars	D. Hooper leg., SMNH colln. 1m, 2f
Fort Qu'Appelle, SK	"carrot"	c. 1977	one larva	R. Hooper leg.(pers. comm.) not emg.
Gypsumville, MB	*Zizia aptera*	1982	? instar	P. Klassen leg. & colln. 1m
Duck Mt. Prov. Park, MB	*Zizia aptera*	23 June 1980	1-2nd, 1-3rd	FAHS leg. & colln. 1f
Duck Mt. Prov. Park, MB	*Zizia aptera*	reared 1982	? instars	J. Troubridge leg. 3m,5f in FAHS colln.
Riding Mt. Nat. Pk., MB	*Zizia aptera* - foodplant determined in Heron & Robinson (1976)	18-25 June 1955	"several hundred eggs and newly hatched larvae" -Remington (1956)	
Riding Mt. Nat. Pk., MB	"wild parsnip" & "meadow parsnip"	2 July 1978	? instars	P. Klassen leg. & colln. 2m, 1f
Riding Mt. Nat. Pk., MB	*Zizia aptera*	21-22 June 1980	11-2nd & 3rds, 1-4th	no emg.
Rid. Mt. Park area, MB	*Zizia aptera*	1982	?inst. (prod. 40 pupae)	H. Kimmich leg. & colln. ?emg.
Rid. Mt. Park area, MB	*Zizia aptera*	19 July 1977	? instars	J. Troubridge leg. & colln. ?emg.
Clan William, MB	"parsnip"	Sept. 1970	? instars	R. Hooper colln. 1m, 1f
Gladstone, MB	*Zizia aptera*	20 June 1983	4-1st & 2nds	P. Klassen leg., FAHS colln. 1m, 1f
Culross, MB	"parsley"	23 July 1977	"mature larva"	P. Klassen leg. & colln. 1m
Culross, MB	*Zizia aptera*	30 June 1982	? instar	P. Klassen leg. & colln. 1f

Personal History

I was born February 21, 1957, in Calgary, Alberta, to Gudrun Claire Sperling (née Seehawer) and Werner Sperling. I have three siblings - an older brother and two younger sisters. Until I was nine years old, we lived on a farm on the northeast edge of Calgary, where I developed an early interest in natural history. Some of my earliest memories are of the thrill of rearing caterpillars, trapping gophers and finding a *Hyalophora gloveri* when I was in my second grade.

In 1966 we moved 50 km to a new farm at Bragg Creek and I found myself in a naturalist's paradise. I began to collect butterflies seriously, as well as filling numerous notebooks with daily butterfly observations and plant flowering times. Both my father and mother always encouraged these pursuits and for several years my mother kept me informed of the butterflies and birds I had missed while I was in school. Her distaste for the rotting rodents and escape-prone caterpillars which I brought into the house was eventually translated into a small shack which my parents built for me and my brother to fill with biological trophies and model airplanes. In high school my interests spread out to encompass such things as boiling the meat off a road killed porcupine in our barn, and surreptitiously tiptoeing along the rafters in an old section of my school, picking torn bits of a century old map out of the insulation. The porcupine skeleton produced both an awesome stench and a successful science fair project, while the eventually-restored map led to a severe reprimand from the principal for breaking through the ceiling, as well as a term paper on the history of Springbank School. My high school biology teacher, Vivian Pharis, was a major source of assistance and encouragement throughout my adolescent years, and I recieved much help from my other teachers as well.

After finishing high school, I went on a collecting trip to the Yukon which resulted in over a dozen flat tires, many rare butterflies, and a confirmed love for travelling. In the fall of 1975 I entered the University of Alberta, where I obtained an honors degree in zoology four years later. I worked for several summers on a number of aspects of farm machinery construction in Calgary, as well as two summers as a research assistant at the Rocky Mountain Biological Laboratory in Colorado, and one summer as a Job Corps leader at the Agriculture Canada research station in Lethbridge. My summers at RMBL led to a renewed zest for field biology, and the discovery of a new alpine nymphalid butterfly. When I finished my bachelors degree, I travelled for five months throughout Europe, a trip that was of small academic but large personal consequence.

I officially began my masters study in the fall of 1980, but in a way it was really begun in 1971, when I discovered an intriguingly unclassifiable population of *Papilio machaon* group swallowtail butterflies behind my parents' farm. I soon became convinced from the apparent ecological and phenotypic unity of these butterflies that they were all part of the same population, and one of the satisfactions of my masters' program has been to demonstrate that more rigorously. Although my study has concentrated on discovering and explaining the patterns of variation in a series of butterfly populations, I feel that it has meant much more to me. In one way it has been like a Rorschach blot, in that my efforts to focus on the outlines of the scientific problem have sometimes produced only a profile of my own psyche. In another way it has been like a Zen koan, where my attempts to resolve the essentially insoluble problem, of how many species there are, has led to an altered way of viewing the academic and biological universes.